NOAA Technical Report NMFS 121 August 1994

Marine Flora and Fauna of the Eastern United States

Platyhelminthes: Monogenea

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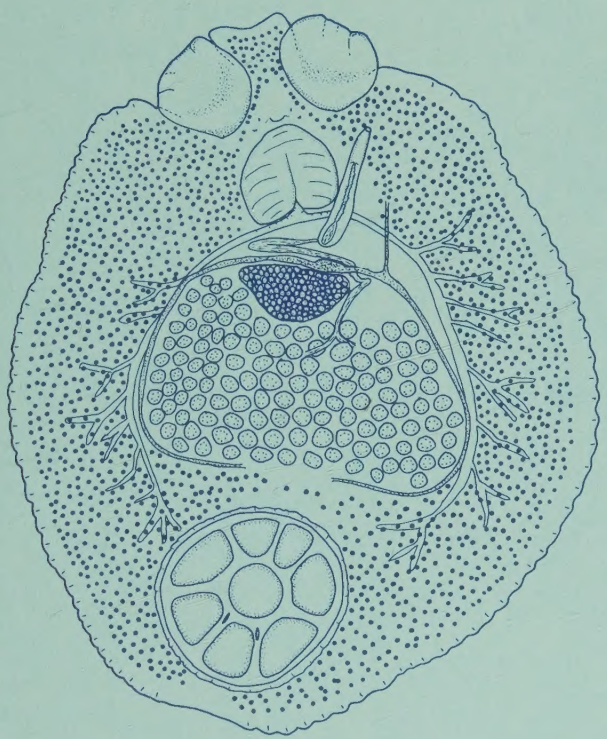

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A Technical Report of the *Fishery Bulletin*

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Platyhelminthes: Monogenea

Sherman S. Hendrix

August 1994

U.S. Department of Commerce
Seattle, Washington

Foreword

This *NOAA Technical Report NMFS* is part of the subseries "Marine Flora and Fauna of the Eastern United States" (formerly "Marine Flora and Fauna of the Northeastern United States"), which consists of original, illustrated, and modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the eastern United States. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation. These manuals are intended for use by students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. They can often serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. Geographic coverage of the "Marine Flora and Fauna of the Eastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Florida, but may vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums.

The "Marine Flora and Fauna of the Eastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual treats a separate major taxon and includes an introduction, illustrated glossary, uniform and originally illustrated keys, an annotated checklist (with available information on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

Marine Flora and Fauna of the Eastern United States Platyhelminthes: Monogenea

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ABSTRACT

This manual includes an introduction to the general biology of the platyhelminth class Monogenea, an illustrated key to the generic level, an annotated systematic list of 108 species in 75 genera and 28 families, a glossary of terms, a host-parasite list, a selected bibliography, and a systematic index. The species listed have been reported on fishes taken in the coastal waters of the northwestern Atlantic Ocean from the U.S.-Canada border to Beaufort, North Carolina. Many of the species, however, have wider geographic distributions that are not reported herein unless adjacent to the geographic area above. In addition, a single species of Neodermata, *Udonella caligorum,* that is found attached to copepods on fish gills is also listed.

Introduction

All monogeneans are parasitic on or, occasionally, parasitic in marine and freshwater fishes, in the urinary bladders of some turtles and amphibians, and on the eye of *Hippopotamus.* Most species are ectoparasitic on the gill filaments of their fish hosts; some are ectoparasitic on fins, on the body surface, in the nostrils, and in the buccal cavity; others are endoparasitic in the esophagus, cloaca, urinary tract, and (in at least one juvenile) the heart. Most monogeneans are highly host specific (Hargis, 1957b), which aids in the specific identification of worms from a particular host. Many of the Monogenea reported from marine and estuarine fishes along the northeastern coast of the United States (Maine to North Carolina) have a more extensive, sometimes cosmopolitan, geographic distribution than is covered in this manual. Only a fraction of potential fish hosts have been reported with these parasites. Because many host species have not yet been examined for these helminths, much remains to be done to expand both geographic ranges and host records for Monogenea.

All known Monogenea are hermaphroditic. Most are oviparous (Kearn, 1986) with a short-lived free-swimming ciliated larva, the oncomiracidium (Llewellyn, 1963, 1968, and 1972). Oncomiracidia of at least three marine species are known to seek their specific hosts primarily by chemotaxis, responding to components in fish mucus (Kearn, 1967, 1973, and 1974a; Whittington and Kearn, 1986 and 1990; Whittington, 1987, a and b). Once attached, larvae shed the ciliated epidermis and, as juveniles, remain in place or migrate to the normal site of development, e.g. the ventral surface skin or gills, where they mature to adults. The "viviparous Monogenea," such as *Gyrodactylus* spp., give birth to non-ciliated larvae, which are transmitted to new hosts by direct contact, either as larvae or adult worms.

The biology of monogeneans found along the U.S. Atlantic coast is still poorly known. Most studies on these worms comprise new species descriptions or surveys that give data on prevalence, intensity of infection, or both (e.g. McMahon, 1963 and 1964; Meyers, 1978), although a few publications deal with the ciliated oncomiracidial stage (e.g. Kingston et al., 1969), microecology (e.g. Suydam, 1971), or pathology (e.g. Lawler, 1977; Overstreet, 1978 and 1992).

Monogenea is now generally recognized as a separate class within the phylum Platyhelminthes, rather than a subclass of the class Trematoda. However, considerable controversy remains in the recognition of evolutionary relationships among the higher taxa within the Monogenea (Bychowsky, 1937 and 1957; Llewellyn, 1970 and 1981; Gusev, 1978; Lebedev, 1979 and 1988; Mamaev and Lebedev, 1979; Lambert, 1980, a and b; Malmberg, 1982, 1986, and 1990; Rohde, 1990; Justine, 1991; Boeger and Kritsky, 1993). To present the marine monogene-

ans in this manual, I generally follow the system proposed by Llewellyn (1970), as modified by Beverley-Burton (1984) for the orders and families found on Canadian hosts. The exceptions are that *Udonella* has been removed from the Turbellaria, the microbothriids assigned to the order Microbothriidea Lebedev, 1988, and the monocotylids assigned to the order Monocotylidea Lebedev, 1988.

Only adult monogeneans are treated in this manual. The free-swimming oncomiracidial stage is not covered except to mention, in the systematic section, those species for which a description has been given. Monogenean species from estuarine and continental shelf fishes are included while species from offshore deep-water fishes are not. The northern extreme of the geographic range covered herein is the U.S.-Canada border; the southern extreme is Beaufort, North Carolina. Many of the monogeneans listed below have a wider geographic distribution. Generally, only those reports from adjacent geographic regions are included; reports from other parts of the globe are not.

Collection and Examination

Collecting monogeneans from freshly caught marine fishes most often involves examining the body surface and fins before removing gills by the following methods:

1. Place the gills in a separate container of dilute formalin, e.g. 1 part concentrated (40% formaldehyde or "100%") formalin to 4,000 parts seawater (Pritchard and Kruse, 1982), which relaxes and fixes the worms with a minimum of contraction or distortion.
2. Examine the fins, skin, scales, buccal cavity, nasal capsules, and cloaca of the fishes for monogeneans.
3. Leave the material in the dilute formalin solution for approximately one hour, which is sufficient time to relax most specimens.
4. Shake the container vigorously for about a minute to dislodge worms.
5. Pour the liquid into a cylinder or other tall container and let it stand for several minutes to allow the worms to settle.
6. Decant the supernatant fluid and examine the sediment in a petri dish under a dissecting microscope.
7. Pipet worms into a fixative, such as 5% formalin or AFA (alcohol-formalin-acetic acid).

An alternative method is to place the heads or whole fish directly into a fixative, such as 10% formalin or AFA, at a proportion of 2–3 parts fixative to 1 part gill material.

Alternative methods for relaxing and isolating worms are given by Pritchard and Kruse (1982). For example, freezing the gills, branchial basket, or even whole fishes for 6–12 hours often aids in preventing mucus production by gill tissues and kills the worms in a relaxed state. However, for studies involving transmission electron microscopy, physiology, or behavior, carefully remove living worms from the host with the aid of a dissecting microscope. For scanning electron microscopy thoroughly wash worms by vigorous shaking in several changes of artificial seawater to remove attached mucus and debris before fixation (Halton, 1974).

After specimens have been in the fixative for 12–24 hours, transfer specimens to vials that contain internal labels and 70% ethanol for storage. However, specimens may be left in the formalin fixative almost indefinitely. Because of the importance of hamuli and marginal hooklets in taxonomy, small monogeneans such as *Gyrodactylus* spp. are usually mounted unstained on slides in glycerol jelly by using a double coverslip method (Pritchard and Kruse, 1982). However, another staining method uses Gormori's trichrome solution with good results (Kritsky et al., 1978).

Treat larger monogeneans in a manner similar to the whole mount preparation techniques employed for digenetic trematodes. After fixing, store the worms in 70% ethanol until stained. Most staining procedures use either alcoholic carmine or aqueous hematoxylin. Several general parasitology laboratory manuals (e.g. Pritchard and Kruse, 1982; Meyer et al., 1992) provide detailed accounts of the fixation, staining, dehydration, clearing, and mounting techniques employed to study these organisms. Cooper (1988) described the preparation of serial sections of platyhelminth parasites, which are useful in tracing the location of ducts and other structures.

Several structures are important for the identification of Monogenea. Most important for identification of monogenean genera is the posterior attachment organ, or haptor, and its associated hard (sclerotized) structures (Figs. 1–4). The shape and nature of the anterior attachment structures, reproductive system, and digestive system are also important in keying out these worms (Figs. 1 and 2). The anterior attachment organ may comprise a pair of concave disklike structures, a pair of buccal suckers, head organs (paired, glandular duct openings), or a single, weak, oral sucker. The number and placement of the testes, presence or absence and shape and number of spines within the male copulatory complex, shape and position of the ovary and uterus, and position of the vagina(e) and genital pore are all useful diagnostic characters. Eggs, when present in the uterus or ootype, can also aid identification. The intestine usually consists of a pair of straight or highly branched ceca that end blindly or are confluent at the posterior end of the body. However, in some of the larger species the intestinal ceca may be obscured by extensive vitellaria. In some taxa the shape of the pharynx is of taxonomic value.

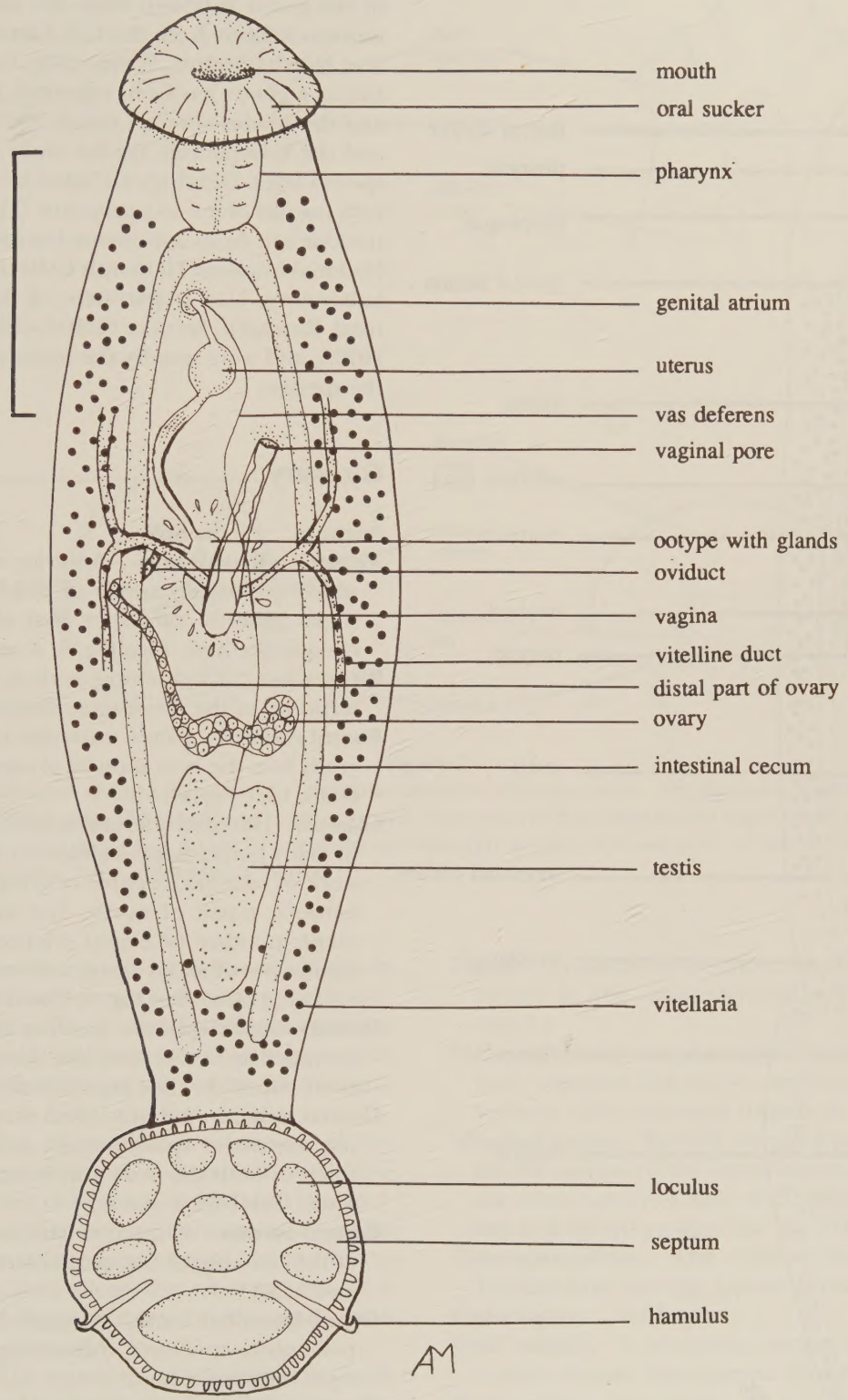


Figure 1

Dasybatotrema dasybatis (family Monocotylidae), generalized composite anatomy, ventral view. Scale: 1 mm.

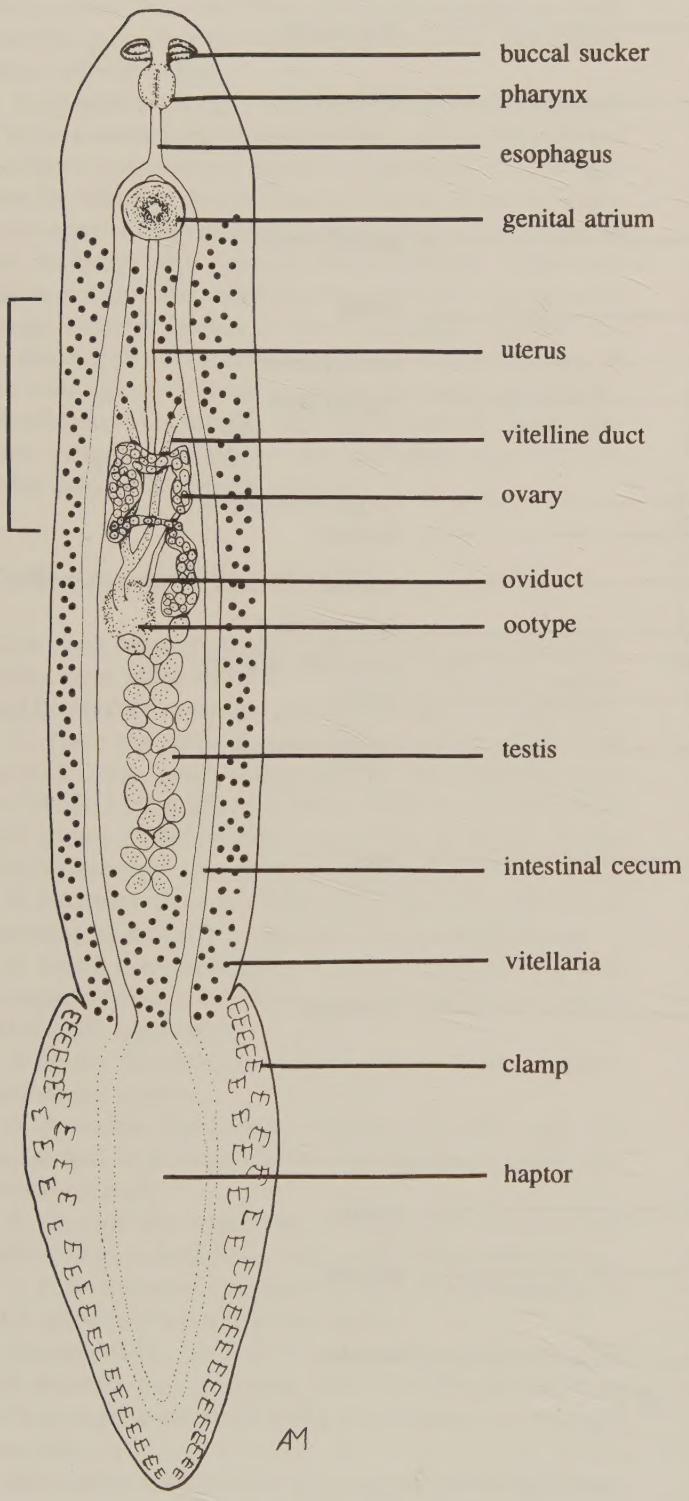


Figure 2
Pauciconfibula pogoniae (family Microcotylidae), generalized composite anatomy, ventral view. Scale: 2 mm.

Monogeneans included in the key of this manual are designated by a specific name when only one member of the genus is known from the coastal waters of the western Atlantic from the U.S.-Canada border to Beaufort, North Carolina. Where more than one representative of a genus has been reported, the key is to genus and the reader should consult the systematic account and the host-parasite list for more information at the species level. Drawings included in the key were made with the aid of a microprojector. The majority of illustrations are from specimens borrowed from the U.S. National Museum Helminth Collection, Biosystematics Laboratory, U.S. Department of Agriculture–Agricultural Research Service (USDA–ARS), Beltsville, MD 20705, and were usually the holotype or a paratype of the species.

Glossary

Anchors. See **hamuli.**

Anterior adhesive area. Anterior attachment organs, which are usually sessile or disklike and produce a sticky adhesive substance that allows the worm to cling to the host. (See Fig. 3, A and B.)

Bifurcation. A branching, such as the intestine at the terminus of the esophagus, divided into two parts.

Buccal suckers. Paired muscular suckers opening laterally into the buccal cavity of some polyopisthocotyleans. (See Fig. 2.)

Clamps. Haptoral sclerotized structures that are found in many polyopisthocotyleans and consist of a framework of sclerites, capable of grasping host gill tissue between a pair of valves. The size, shape, arrangement, number of clamp sclerites, and number of clamps are of major taxonomic importance in differentiating taxa. (See Fig. 4, C and D.)

Dorsal marginal spines. Small spines of various shapes arranged in rows along the dorsal body margin in some capsalids. (See Figs. 12B and 13B.)

Genital atrium. A cavity, often muscular and containing distinctive spines, which receives the terminal ducts of both the male and female reproductive systems. (See Figs. 1 and 2.)

Genital corona. Clusters or circles of spines within or at the opening of the genital atrium. (See Figs. 47B and 71B.)

Genito-intestinal canal. A small duct, found only in polyopisthocotyleans, connecting the oviduct to the right intestinal cecum.

Hamuli. The paired sclerotized hooklike structures of the haptor. The hamuli are movable and attach the parasite to the host. Much of the American literature refers to these structures as anchors. (See Figs. 1 and 3, C and D.)

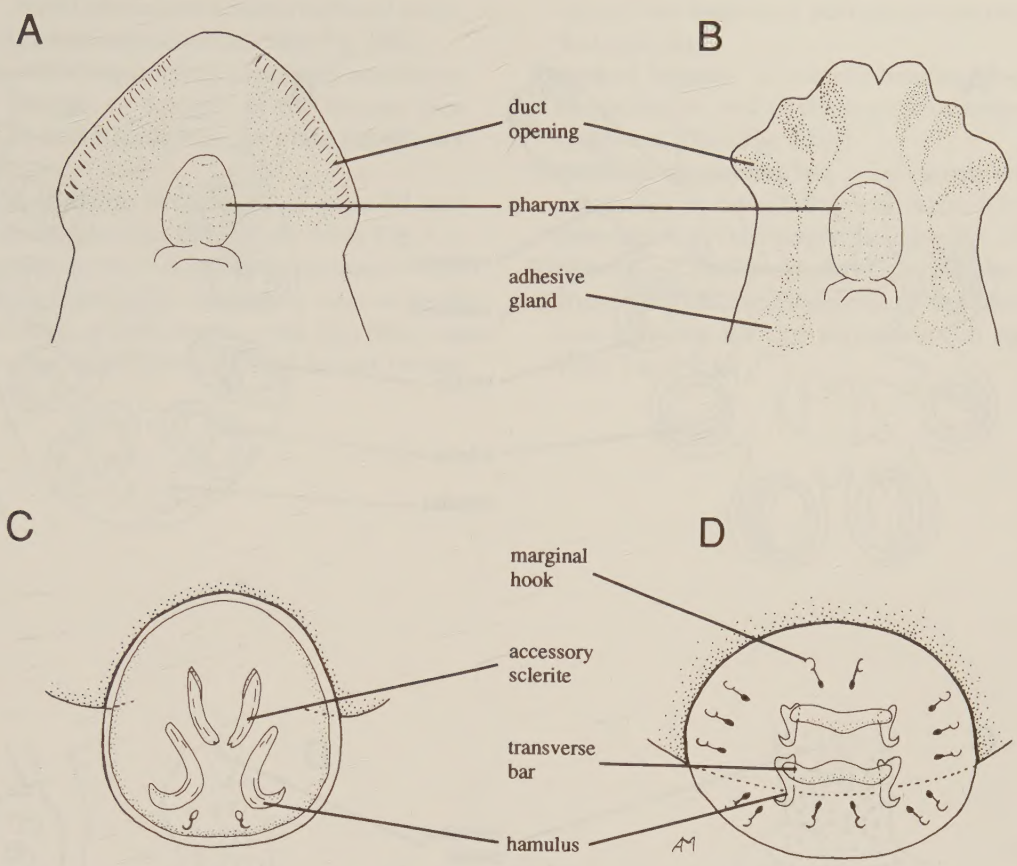


Figure 3
Undivided disklike haptors and glandular anterior adhesive areas: (**A**) glandular anterior adhesive area; (**B**) anterior adhesive area with three pairs of head organs; (**C**) haptor with two pairs of hamuli and a pair of accessory sclerites; (**D**) haptor with two pairs of hamuli, two transverse bars, and marginal hooks.

Haptor. The posterior attachment organ which usually carries additional components such as marginal hooks, hamuli, accessory sclerites, armed suckers, or clamps. The structure and its hard parts are of major taxonomic importance in differentiating the orders, families, and genera. (See Figs. 1, 2, 3, C and D, 4, A–D.)

Haptoral appendix. A muscular extension of the haptor having two terminal suckers and usually hamuli, characteristic of hexostomatids. (See Fig. 4A.)

Head organ. Groups of anterolateral postpharyngeal glands that open via the head organs and produce a sticky secretion that allows the anterior end of a worm to adhere temporarily to the host while feeding. (See Fig. 3, A and B.)

Intestinal ceca. The intestine, which can be a single (=cecum) unbranched tube ending blindly (see Fig. 8), two (=ceca) unbranched or highly branched tubes that may end blindly (see Fig. 9), or be posteriorly confluent (see Fig. 16). Ceca are sometimes obscured by extensive vitellaria (see Fig. 21).

Loculi. Haptoral depressions, usually limited by septa, found in the capsalids and monocotylids. (See Fig. 1.)

Male copulatory complex (apparatus). An often muscular complex that may be armed with a sclerotized stylet or other accessory structures. (See Fig. 82D.)

Marginal hooks. Radially arranged pairs of small hooks on the margin of the larval haptor, which persist in the adult haptor of many taxa, such as the gyrodactylids and dactylogyrids. (See Fig. 3D.)

Oncomiracidium. The ciliated larval stage, which hatches from the egg, typical of the Monogenea.

Opisthaptor. See **haptor**.

Oral sucker. A muscular sucker surrounding the mouth of some Monogenea. (See Fig. 1.)

Pedunculate. Descriptive of a structure borne on a stalk. (See Fig. 52.)

Peduncular bar. A sclerotized transverse bar, which is usually pitted and found immediately anterior to the haptor in some gyrodactylids. (See Fig. 34.)

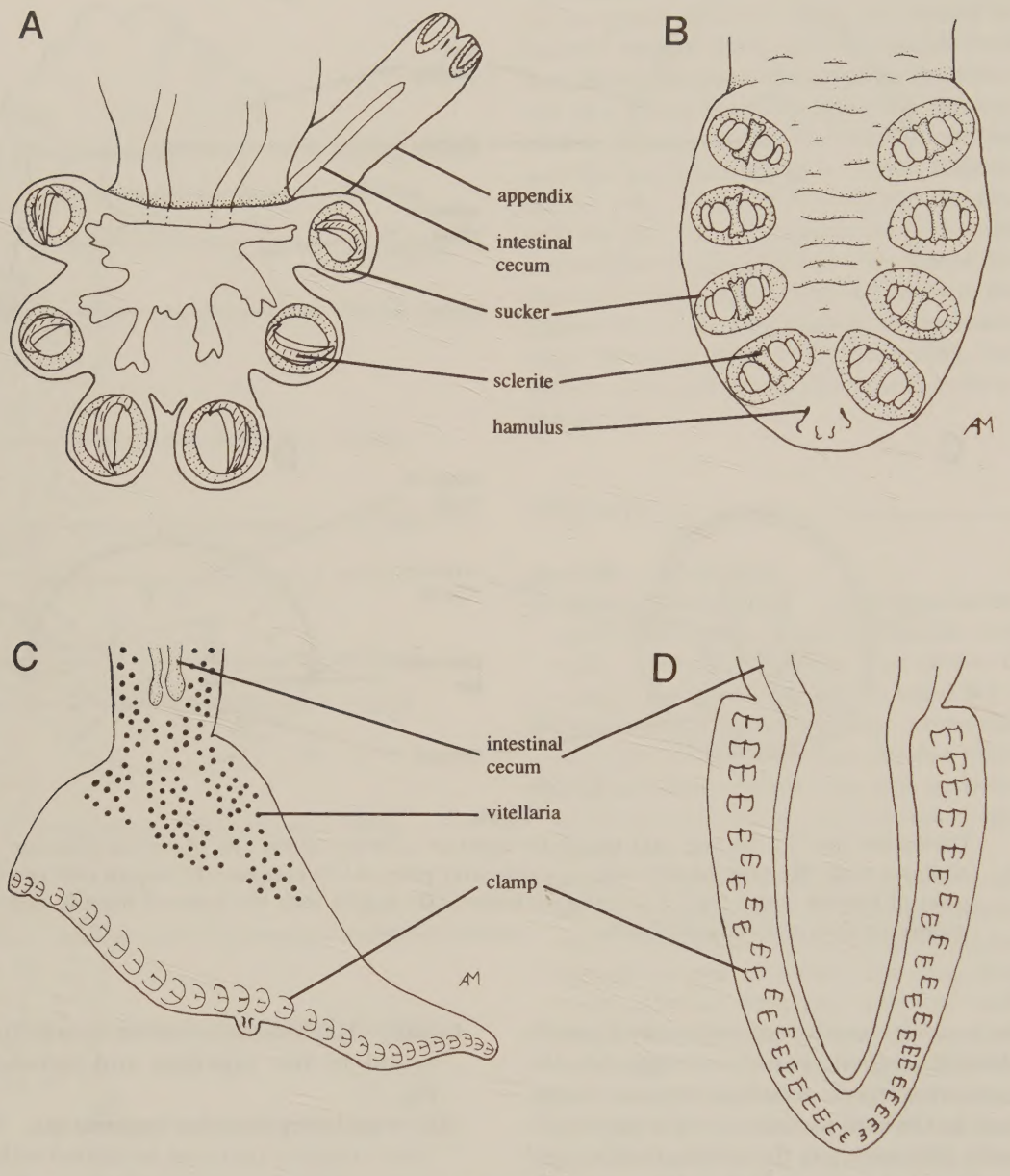


Figure 4

Representative polyopisthocotylean haptors: (**A**) haptor with appendix and three pairs of pedunculate suckers, each containing a sclerite; (**B**) haptor with four pairs of sessile suckers, each containing sclerites; (**C**) asymmetric haptor with multiple clamps; (**D**) symmetric haptor with multiple clamps.

Pharynx. A muscular pumping organ lying between the mouth and esophagus that aids in ingestion of food. (See Figs. 1 and 11, A and B.)

Preoral suckers. A pair of weakly muscular disklike structures just anterior and lateral to the mouth. See **anterior adhesive organs** above. (See Fig. 12A.)

Prohaptor. An obsolete term for the unarmed holdfast organ (**anterior adhesive area**) at the anterior end of the body bearing suckers and glands or both. The nature of this organ is of taxonomic value. (See Fig. 3, A and B.)

Pseudohaptor. A functional posterior organ characteristic of *Pseudacanthocotyla*, which is not derived from the larval haptor but which develops just anterior to it. (See Fig. 5.)

Pseudosucker. A weakly muscular, funnel-like structure surrounding the mouth. It may contain glandular openings around the margin as in *Dasybatotrema*. (See Fig. 24A.)

Ridge sclerites. Small sclerotized structures found in the rims of loculi in some monocotylids. (See Fig. 26C.)

Sclerites. Sclerotized supporting structures associated with hamuli, clamps, or suckers of the haptor (see Fig. 3C and 4, A and B), vaginae, or male copulatory complex.

Septa. Ridges that divide the haptor of capsalid and monocotylid monogeneans into loculi. (See Fig. 1.)

Squamodisc. A circular or oval structure associated with the haptor and consisting of concentric rows of small spines characteristic of diplectanids. (See Fig. 36B.)

Suckers. Muscular attachment devices found primarily on the haptor of polyopisthocotyleans. (See Fig. 4, A and B.)

Terminal lappet. A sclerite-bearing flap of tissue at the posterior end of the haptor of some polyopisthocotyleans. (See Fig. 65C.)

Transverse supporting bar. Transverse sclerotized bars associated or articulating with hamuli in many monogeneans, e.g. Dactylogyrida. (See Fig. 3D.)

Vitellaria. Usually extensive glands that produce nutrients for the development of the oncomiracidium and proteins for the formation of eggshells. (See Figs. 1 and 2.)

Key to the Monogenea Parasitic on Marine Fishes of the Eastern United States

1 Haptor well developed, undivided and disklike, with or without hamuli; haptoral suckers and clamps absent; anterior adhesive area usually with glands opening via head organs, bilobed sessile, or disklike areas (see Fig. 3, A and B) **2**

1 Haptor divided, usually with 4 or more pairs of suckers or clamps, pedunculate or sessile, hamuli present or absent; anterior region containing buccal suckers or weak oral sucker (see Figs. 2 and 4, A–D.) ..... **(Order Polyopisthocotylida) 39**

2(1) Posterior attachment organ a pseudohaptor with numerous radiating rows of spines, larval haptor with 16 marginal hooks, undeveloped, at posterior margin of pseudohaptor. Parasitic on skates (Rajidae) ..... **(Family Acanthocotylidae)** ***Pseudacanthocotyla verrilli*** **(Fig. 5)**

2(1) Posterior attachment organ a haptor lacking radial rows of spines **3**

3(2) Haptor distinctly muscular, disklike, with or without 1 or 2 pairs of hamuli and anterior sclerotized accessory sclerites and lacking transverse supporting bars; anterior adhesive area disklike or glandular (see Fig. 6) **4**

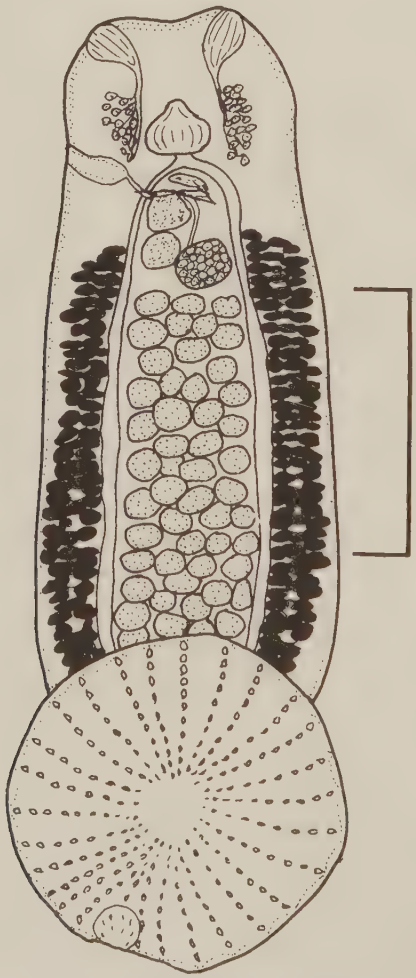


Figure 5
Pseudacanthocotyla verrilli, ventral view.
Scale: 1 mm. Drawn from USNM 7175.

3(2) Haptor a membranous disk, with 1 or 2 pairs of hamuli, each pair supported by a transverse bar; anterior adhesive area glandular (see Fig. 7) **27**

4(3) Intestine with unbranched cecum. Usually parasites of ectoparasitic copepods on fish gills, rarely attached to gill tissue. ..... **(Class Udonellidea, Family Udonellidae)** ***Udonella caligorum*** **(Fig. 8)**

4(3) Intestine with 1 or 2 ceca, unbranched or diverticulate. Parasites of fishes and not crustacea **5**

5(4) Haptor disklike, with or without septa, hamuli usually present. **6**

5(4) Haptor small and muscular, lacking septa and hamuli. Parasitic on requiem sharks (Carcharhinidae). ..... **(Family Microbothriidae) 25**

6(5) Intestine with 2 ceca with numerous diverticula. Usually parasitic on teleosts and, occasionally, elasmobranchs. ..... **(Family Capsalidae) 7**

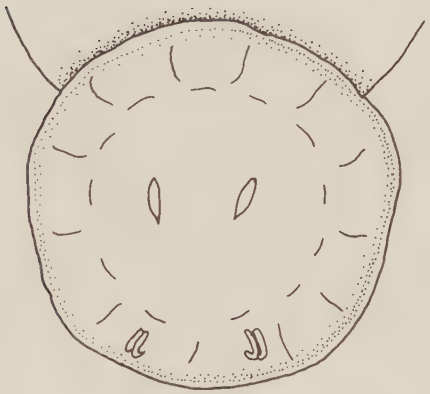


Figure 6
Muscular haptor with two pairs of hamuli and a pair of accessory sclerites.

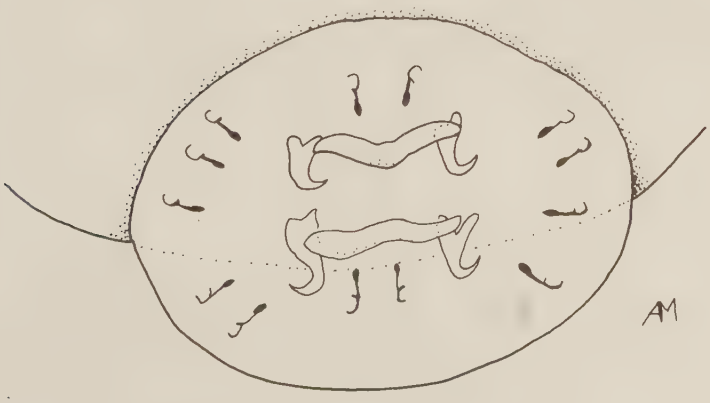


Figure 7
Haptor with two pairs of hamuli, each supported by a transverse bar, and marginal hooks.

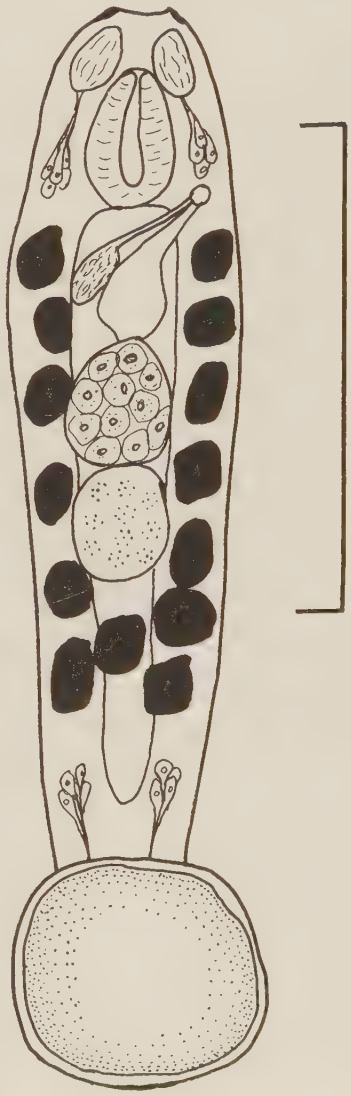


Figure 8
Udonella caligorum, ventral view. Scale: 0.5 mm. After Price (1938b).

6(5) Intestine with 1 or 2 unbranched ceca. Parasitic on elasmobranchs. 16

7(6) Testes 2. 8

7(6) Testes more than 2. 9

8(7) Haptor aseptate, with papillae in posterior half; anterior adhesive area sessile. Parasitic on the roughtail stingray, *Dasyatis centroura*, and Atlantic halibut, *Hippoglossus hippoglossus* . . . ***Entobdella* spp. (Fig. 9)**

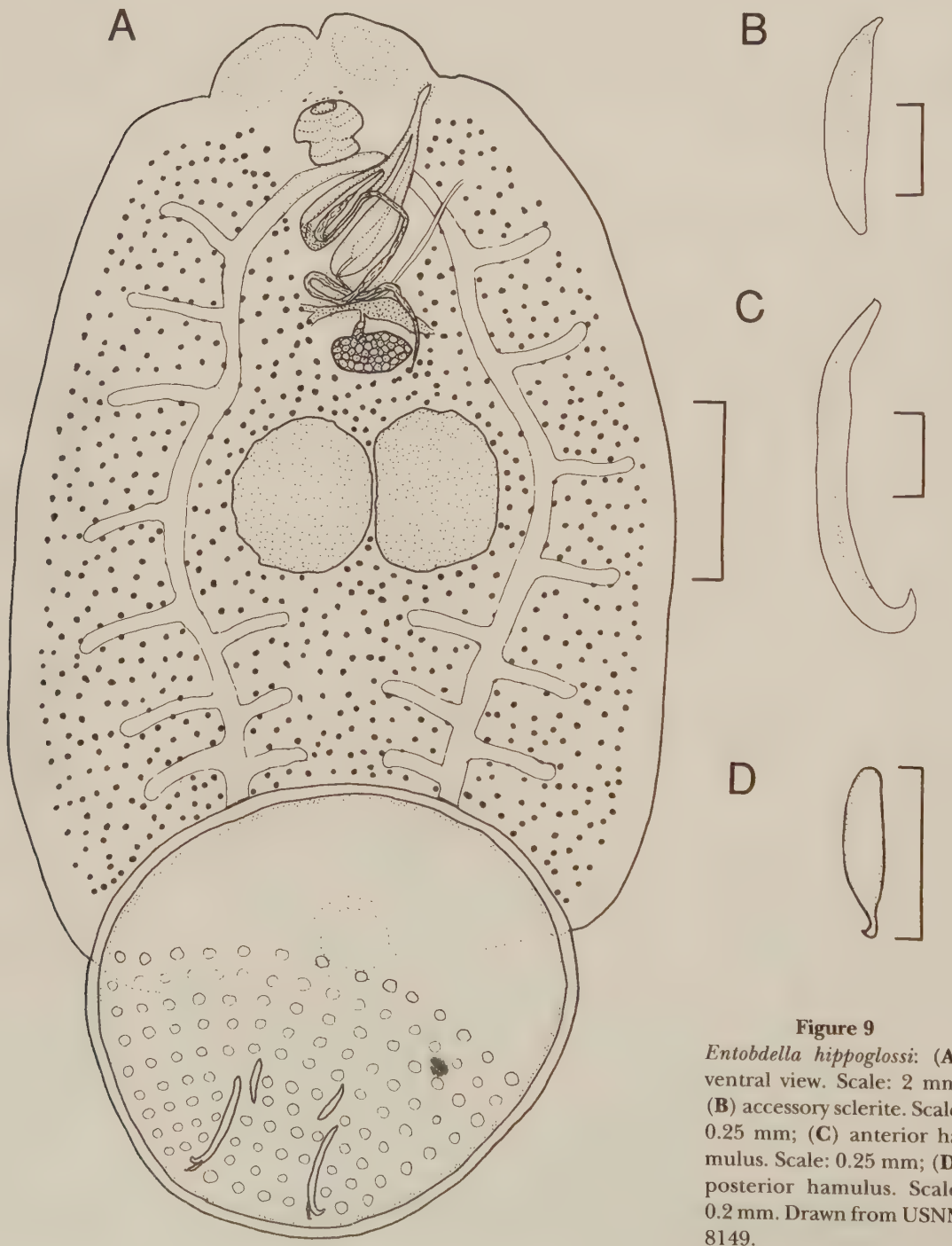


Figure 9
Entobdella hippoglossi: (**A**) ventral view. Scale: 2 mm; (**B**) accessory sclerite. Scale: 0.25 mm; (**C**) anterior hamulus. Scale: 0.25 mm; (**D**) posterior hamulus. Scale: 0.2 mm. Drawn from USNM 8149.

8(7) Haptor aseptate, lacking papillae; anterior adhesive area disklike. Parasitic on the cownose ray, *Rhinoptera bonasus*. ..... ***Benedeniella posterocolpa*** **(Fig. 10)**

9(7) Pharynx constricted near middle (see Fig. 11A). **10**

9(7) Pharynx not constricted (see Fig. 11B). **14**

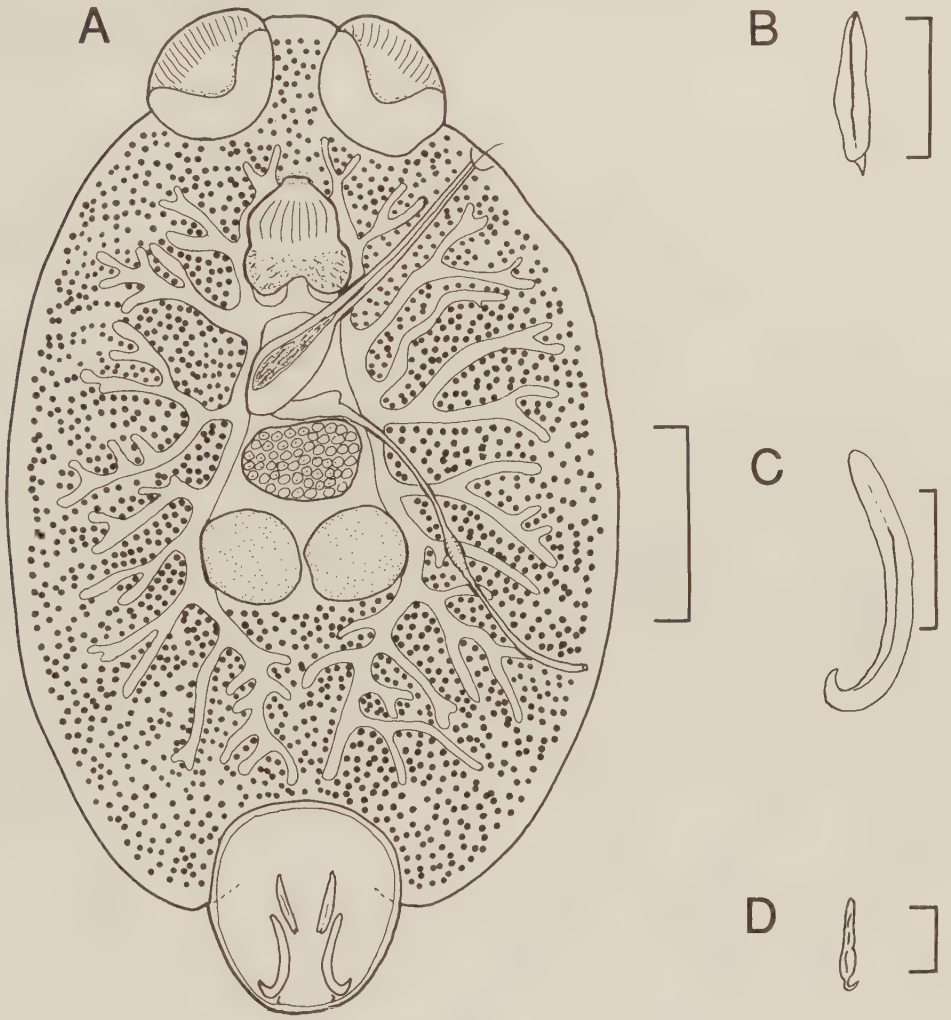


Figure 10

Benedeniella posterocolpa: (**A**) ventral view. Scale: 2 mm; (**B**) accessory sclerite. Scale: 0.5 mm; (**C**) anterior hamulus. Scale: 0.5 mm; (**D**) posterior hamulus. Scale: 0.2 mm. Drawn from USNM 38146.

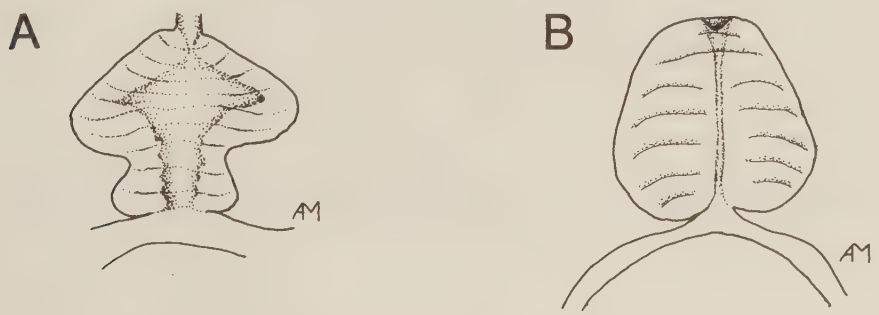


Figure 11

Pharynx shapes: (**A**) constricted; (**B**) not constricted.

10(9) Testes extend laterally to intestinal diverticula. **11**

10(9) Testes confined to intracecal area; parasitic on tunas (Scombridae). **13**

11(10) Ratio of disklike anterior adhesive area diameter to haptor diameter is 1:2; one pair of accessory sclerites present in septate haptor. Parasitic on Istiophoridae and Scombridae.
. . . . . ***Tristomella* spp. (Fig. 12)**

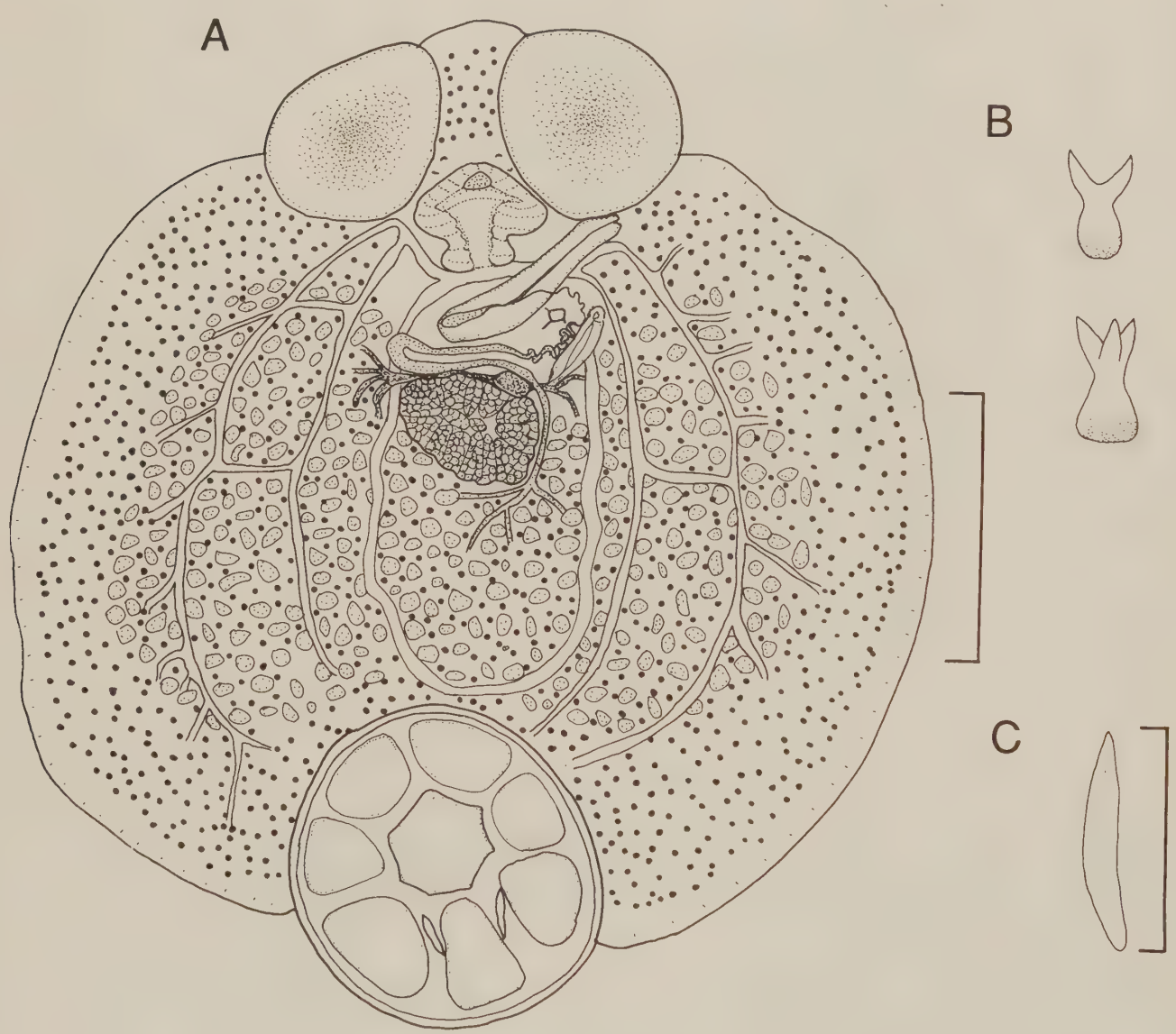


Figure 12
Tristomella laevis: (**A**) ventral view. Scale: 3 mm; (**B**) dorsal marginal spines; (**C**) hamulus. Scale: 0.55 mm. Drawn from USNM 18874.

11(10) Ratio of diameter of suckerlike anterior adhesive area to haptor diameter less than 1:3; hamuli and sclerites absent. **12**

12(11) Ratio of diameter of anterior adhesive area to haptor diameter approximately 1:4. Parasitic on ocean sunfish, *Mola mola*. . . . . ***Capsala martinierei*** **(Fig. 13)**

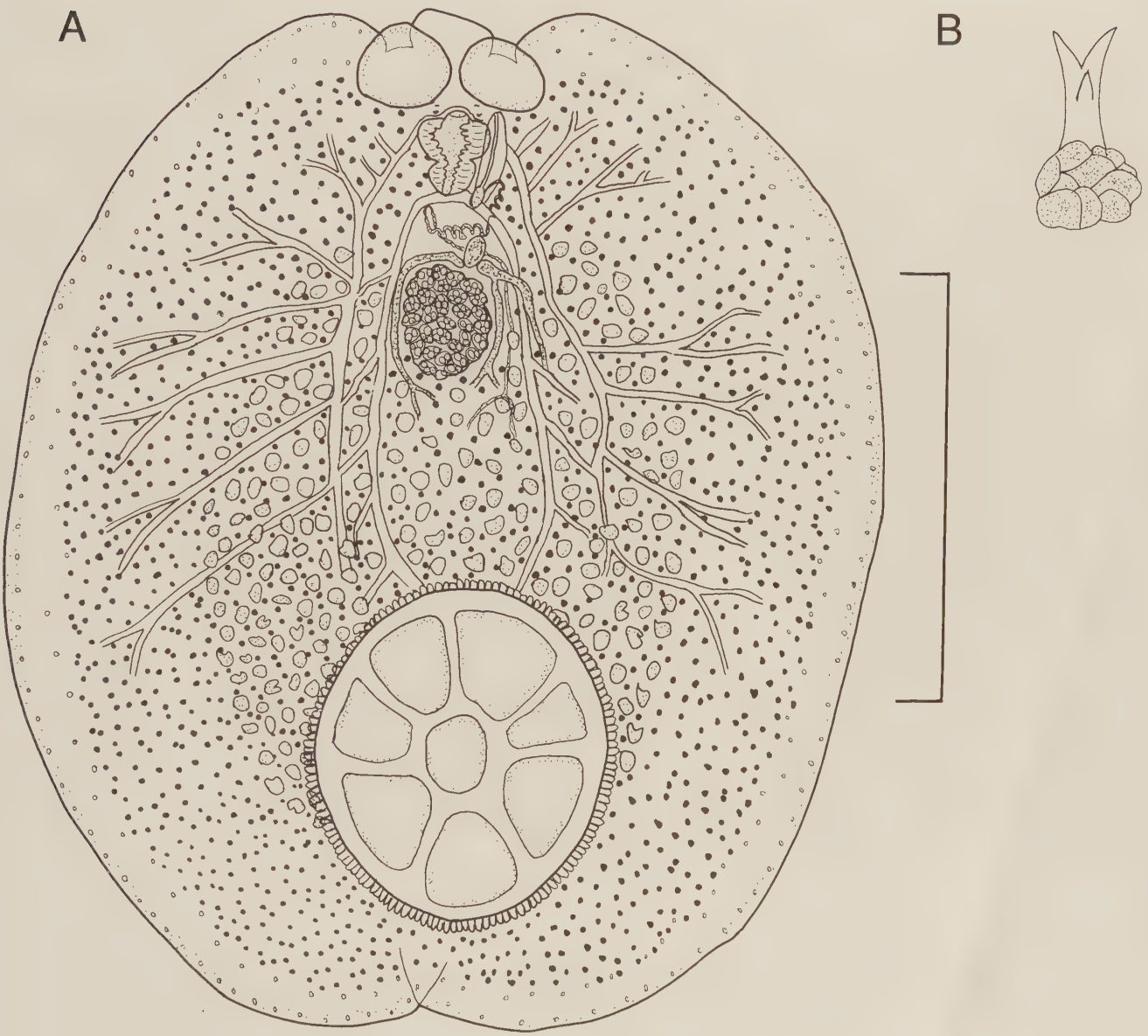


Figure 13
Capsala martinierei: (**A**) ventral view. Scale: 10 mm; (**B**) dorsal marginal spines. Drawn from USNM 41146.

12(11) Ratio of diameter of anterior adhesive area to haptor diameter from 1:5 to 1:6. Parasitic on ocean sunfish ..... ***Tricotyla molae*** **(Fig. 14)**

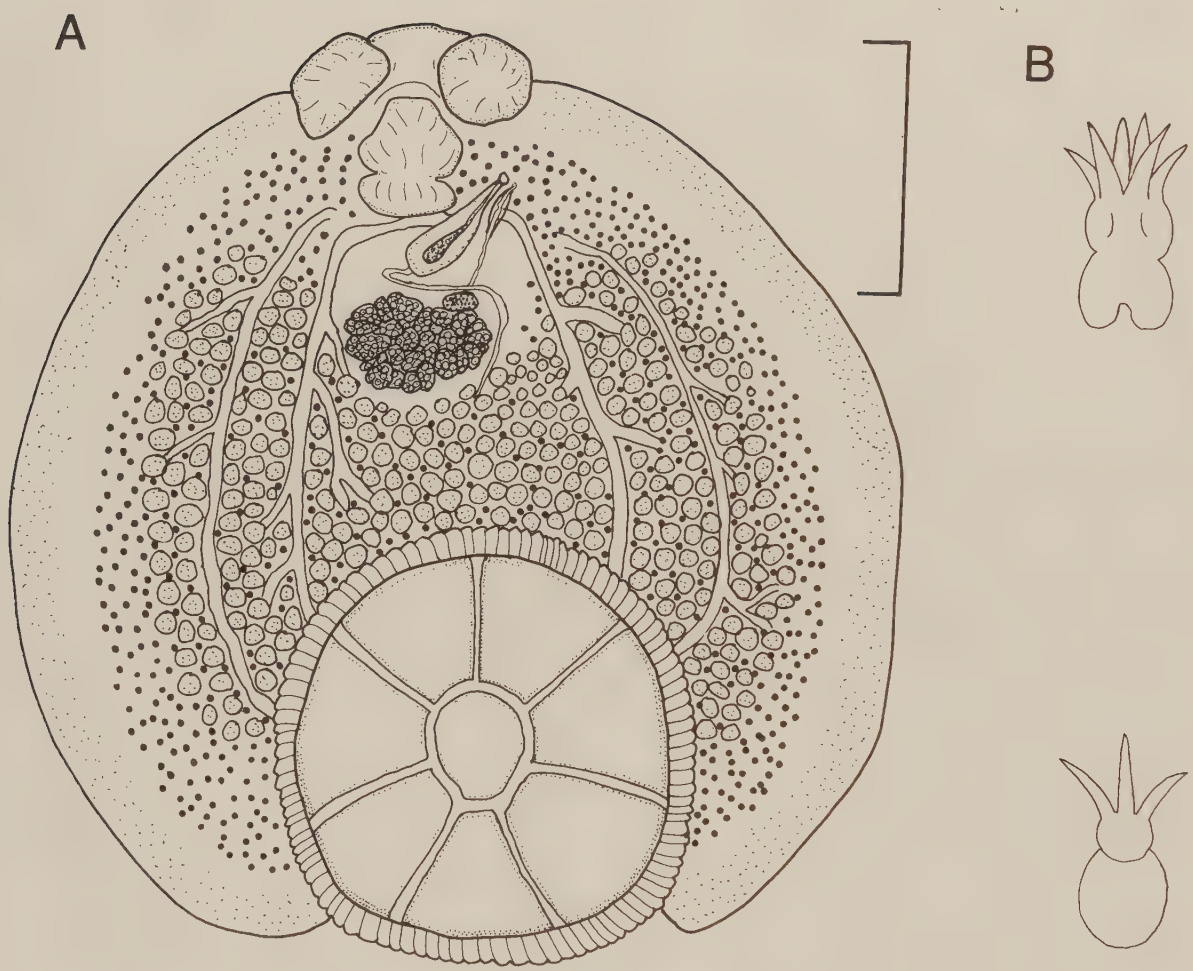


Figure 14
Tricotyla molae. (**A**) ventral view. Scale: 3 mm; (**B**) dorsal marginal spines. Drawn from USNM 8152.

13(10) Parasitic in nasal capsules of tunas (Scombridae) ..... *Nasicola klawei* (Fig. 15)

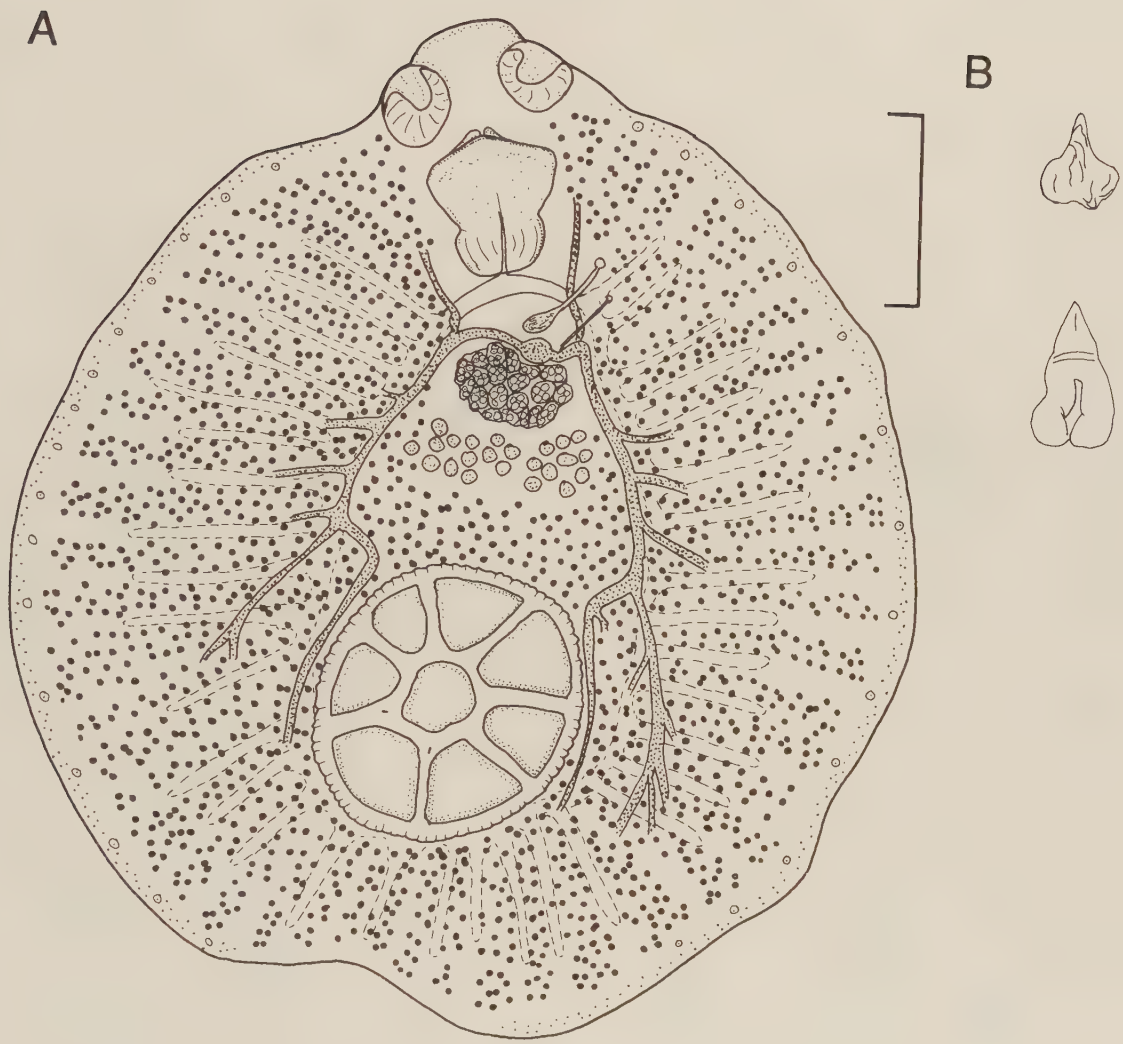


Figure 15
Nasicola klawei: (**A**) ventral view. Scale: 2 mm; (**B**) dorsal marginal spines. Drawn from USNM 59865.

13(10) Parasitic on gills of little tunny, *Euthynnus alletteratus*. . . . . ***Caballerocotyla manteri* (Fig. 16)**

14(9) Haptor aseptate; anterior adhesive area with 2 shallow grooves. Parasitic on sturgeons, *Acipenser* spp. . . . . ***Nitzschia* spp. (Fig. 17)**

14(9) Haptor septate; anterior adhesive area suckerlike or disklike. **15**

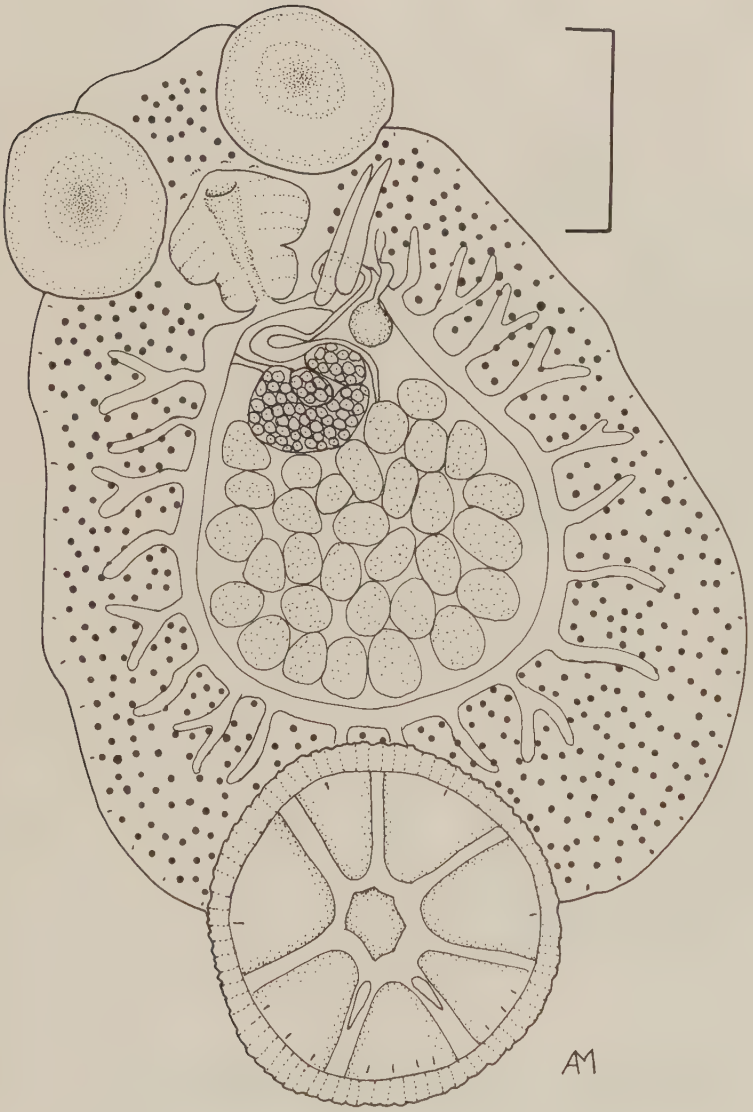


Figure 16
Caballerocotyla manteri: ventral view. Scale: 0.5 mm. Drawn from USNM 37228.

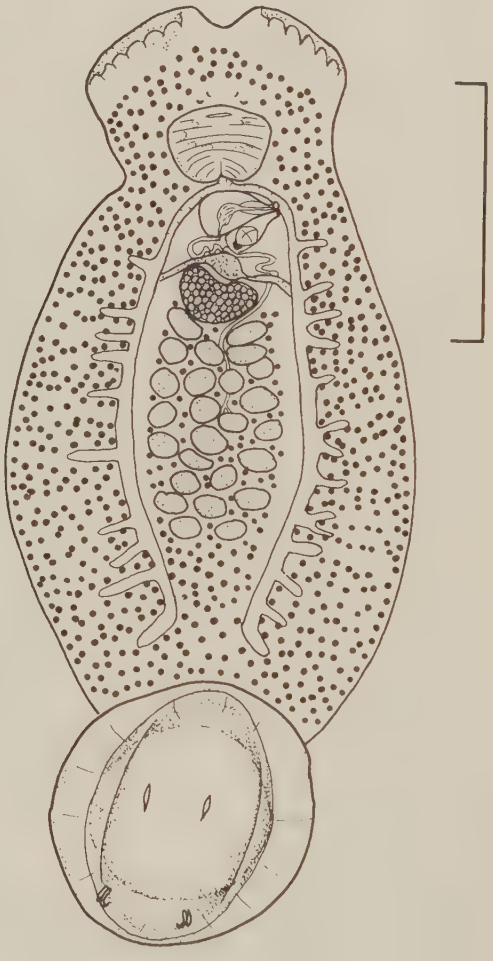


Figure 17
Nitzschia sturionis: ventral view. Scale: 3 mm. Drawn from USNM 73135.

15(14) Haptor with 7 marginal and 1 central loculi; dorsal marginal spines serrated or bifid. Parasitic on swordfish, *Xiphias gladius*, and smooth hammerhead, *Sphyrna zygaena*. . . . . ***Tristoma* spp. (Fig. 18)**

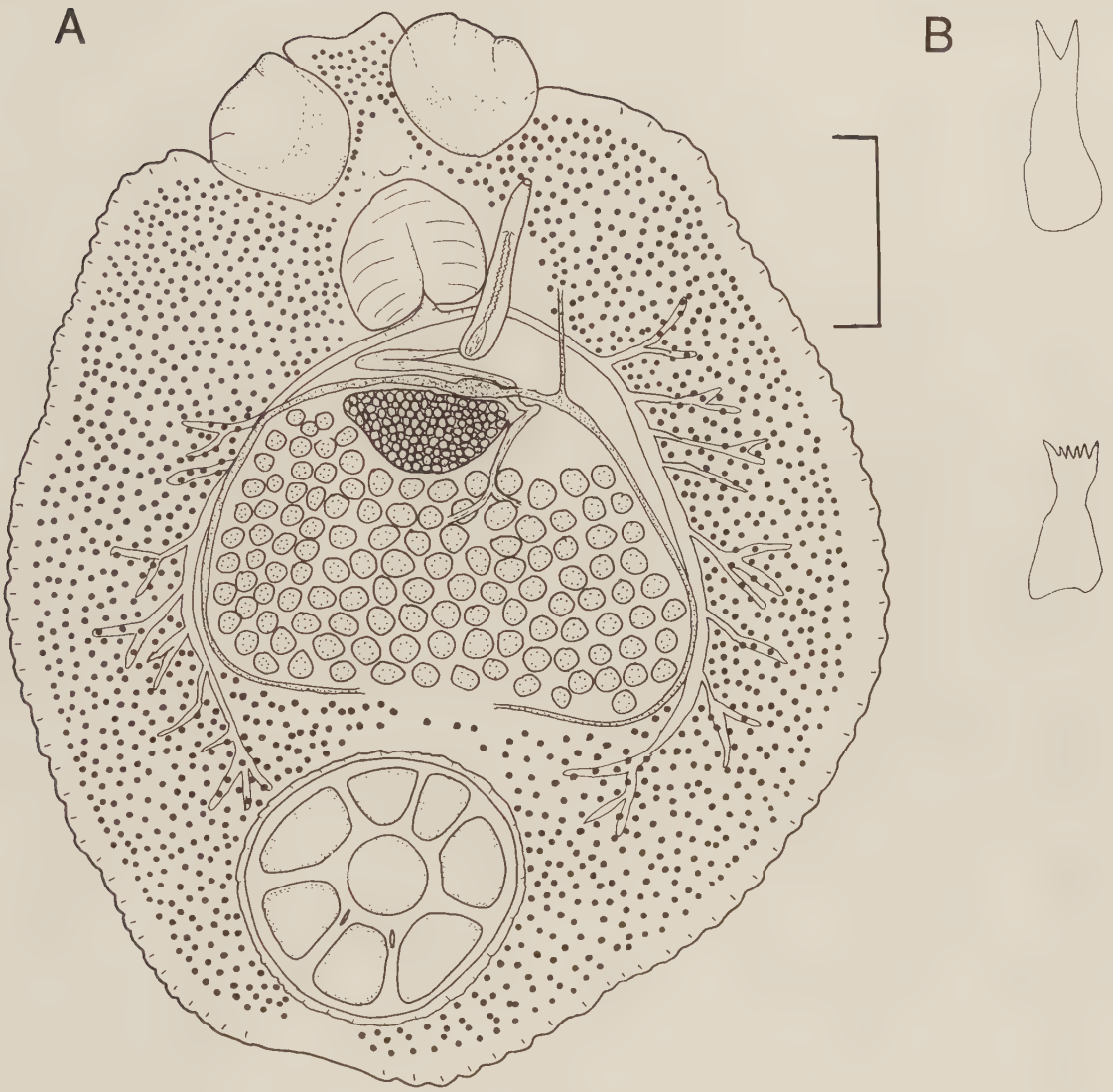


Figure 18
Tristoma coccineum: (**A**) ventral view. Scale: 2 mm; (**B**) dorsal marginal spines. Drawn from USNM 35645.

15(14) Haptor with 9 marginal and 1 central loculi; dorsal marginal spines wider than long, with numerous small cusps. Parasitic on white marlin, *Tetrapturus albidus*. ..... ***Capsaloides* spp. (Fig. 19)**

16(6) Testes 2 or more, tandem. **23**

16(6) Testis 1. Parasitic on elasmobranchs. ..... **(Family Monocotylidae) 17**

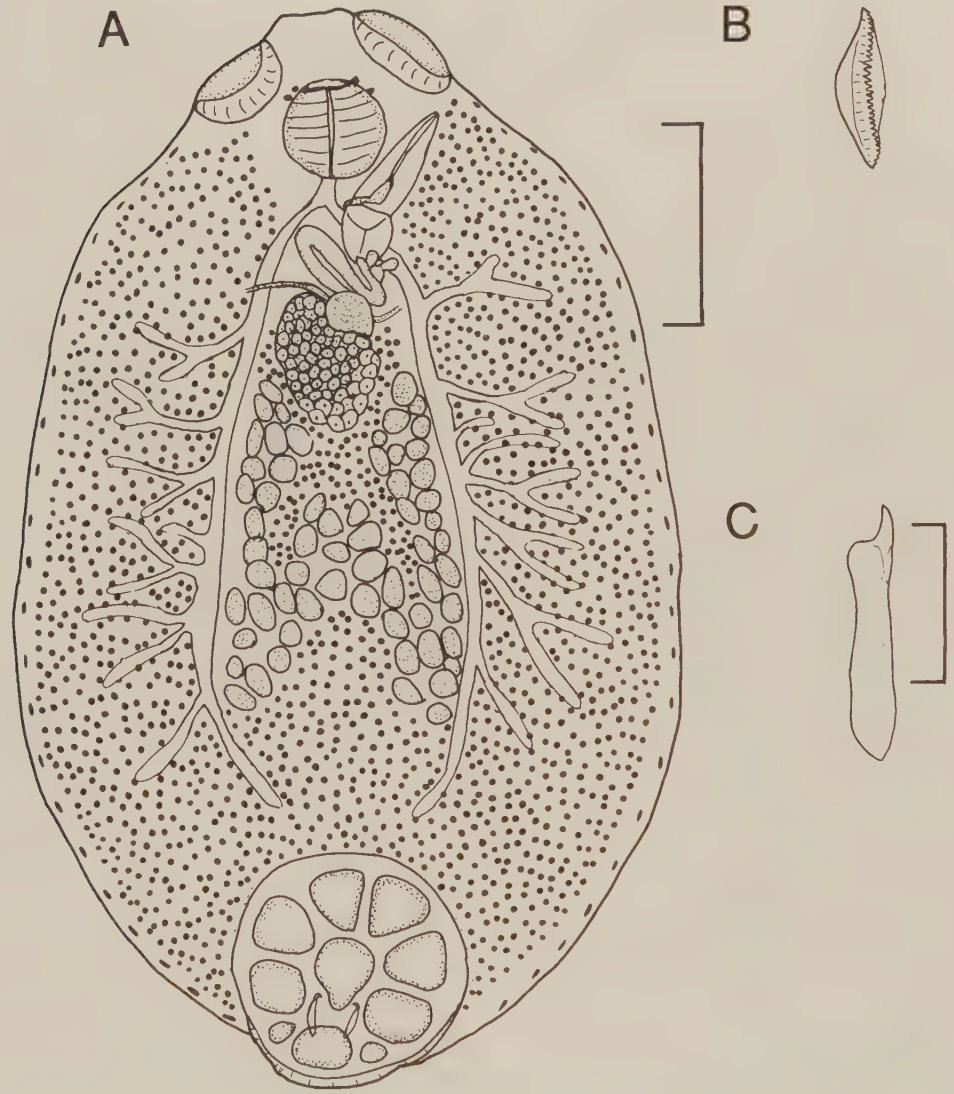


Figure 19

Capsaloides cornutus: (**A**) ventral view. Scale: 1 mm; (**B**) dorsal marginal spine; (**C**) hamulus. Scale: 0.01 mm. Drawn from USNM 35136.

17(16) Haptor septate, with more than 20 loculi. Parasitic on lamniform sharks. . . ***Cathariotrema selachii*** **(Fig. 20)**

17(16) Haptor septate, with 20 or fewer loculi. Parasitic on rays (Dasyatidae) and skates (Rajidae). **18**

18(17) Haptor with 18 or 20 loculi. **19**

18(17) Haptor with fewer than 12 loculi. **20**

19(18) Haptor with 20 loculi, hamuli absent. Parasitic on skates, *Raja* spp. . . . . ***Empruthotrema raiae*** **(Fig. 21)**

Figure 20
Cathariotrema selachii: (**A**) ventral view. Scale: 1 mm; (**B**) hamulus. Scale: 0.1 mm. Drawn from USNM 35674.

Figure 21
Empruthotrema raiae: ventral view. Scale: 0.3 mm. Drawn from USNM 35160.

19(18) Haptor with 18 loculi and 1 pair of large distally recurved hamuli. Parasitic on the roughtail stingray and little skate, *Raja erinacea*. ..... ***Thaumatocotyle dasybatis*** **(Fig. 22)**

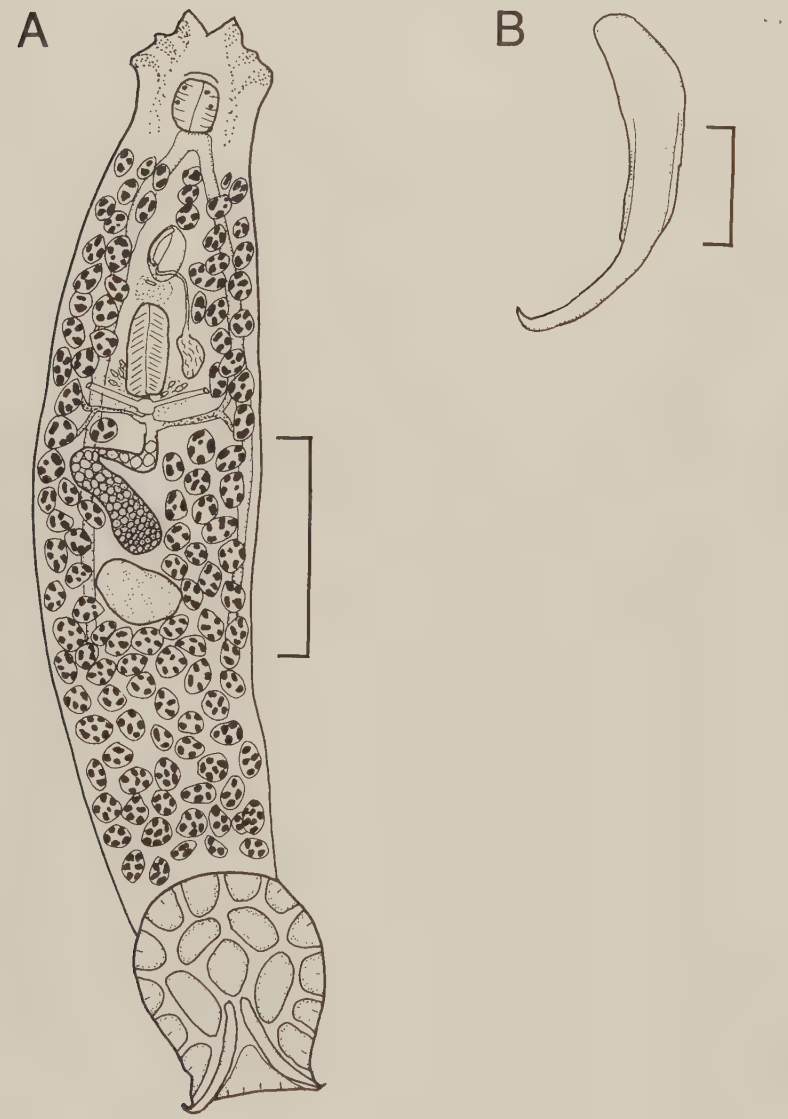


Figure 22
Thaumatocotyle dasybatis: (**A**) ventral view. Scale: 0.5 mm; (**B**) hamulus. Scale: 0.1 mm. Drawn from USNM 35660.

20(18) Haptor with 1 central and 10 peripheral loculi, the most posterior pair with 12 muscular papillae on dorsal surface. Parasitic on the spotted eagle ray, *Aetobatis narinari*. . . . . ***Papillicotyle floridana*** **(Fig. 23)**

20(18) Haptor with fewer than 11 loculi, papillae absent. **21**

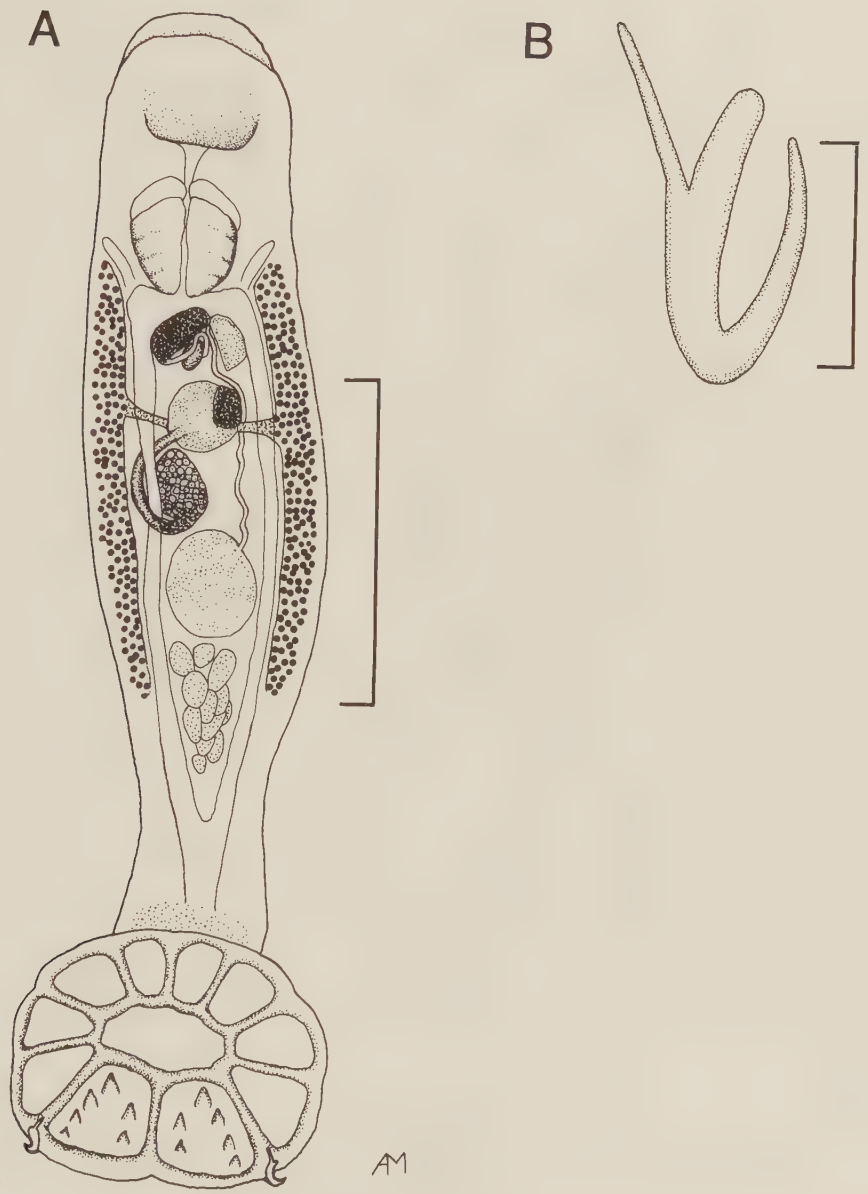


Figure 23
Papillicotyle floridana: (**A**) ventral view. Scale: 0.5 mm; (**B**) hamulus. Scale: 0.025 mm. Drawn from USNM 49447.

21(20) Haptor with 1 central and 7 peripheral loculi, with numerous marginal papillae on rim of haptor, ridge sclerites or sinuous sclerotized ridge absent. Parasitic on the roughtail stingray. ..... ***Dasybatotrema dasybatis* (Fig. 24)**

21(20) Haptor with 1 central and 8 peripheral loculi, marginal papillae absent, ridge sclerites or sinuous sclerotized ridge present. **22**

Figure 24
Dasybatotrema dasybatis: (**A**) ventral view. Scale: 1 mm; (**B**) hamulus. Scale: 0.1 mm. Drawn from USNM 35656.

22(21) Haptor with sinuous sclerotized ridge on septa. Parasitic on the roughtail stingray and spiny dogfish, *Squalus acanthias*. . . . . ***Heterocotyle minima*** **(Fig. 25)**

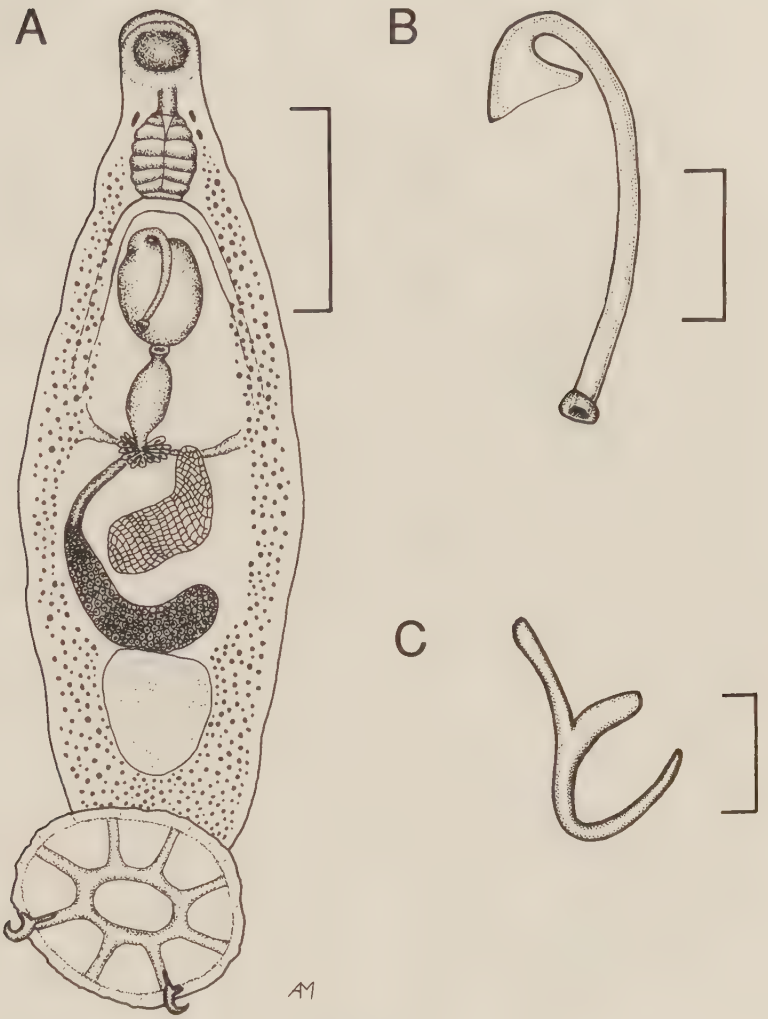


Figure 25
Heterocotyle minima: (**A**) ventral view. Scale: 0.2 mm; (**B**) penis stylet. Scale: 0.025 mm; (**C**) hamulus. Scale: 0.05 mm. Drawn from USNM 35651.

22(21) Haptor with numerous ridge sclerites on septa and rim. Parasitic on stingrays, *Dasyatis* spp. ..... ***Monocotyle* spp. (Fig. 26)**

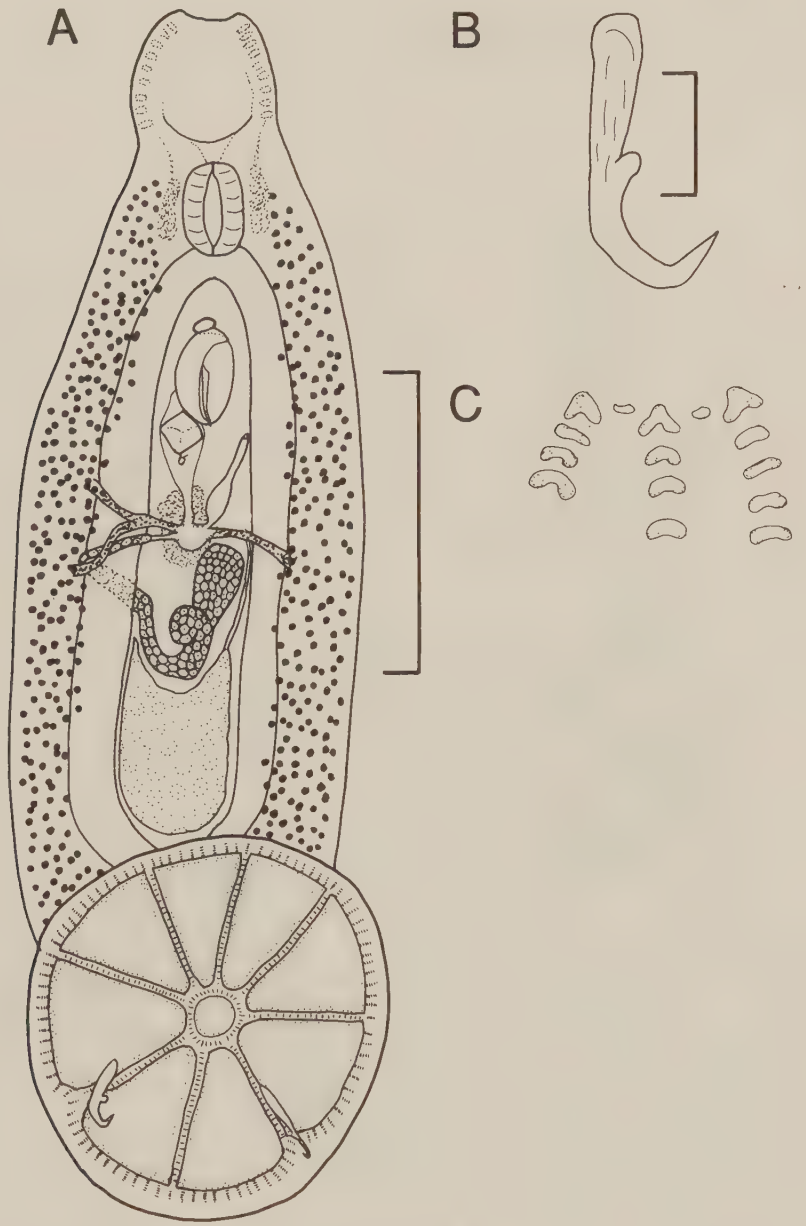


Figure 26

Monocotyle diademalis: (**A**) ventral view. Scale: 0.5 mm; (**B**) hamulus. Scale: 0.05 mm; (**C**) ridge sclerites. Drawn from USNM 49349.

23(16) Haptor septate; anterior adhesive area glandular with numerous ducts. Parasitic on remoras (Echeneidae). ..... ***Dionchus* spp. (Fig. 27)**

23(16) Haptor lacking septa; anterior adhesive area with few gland ducts. Parasitic on elasmobranchs. ..... **(Family Loimoidae) 24**

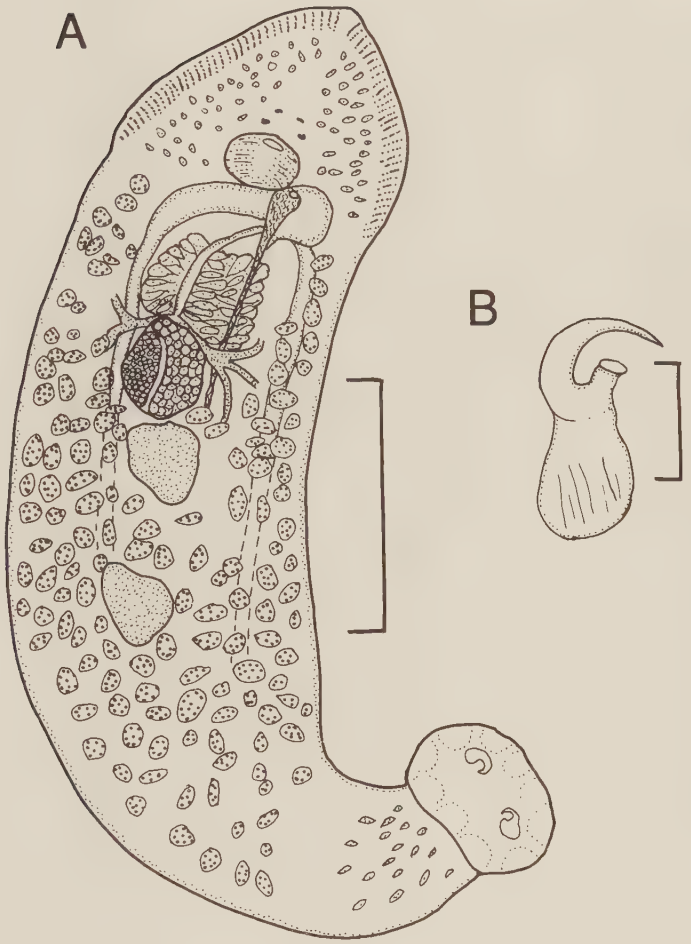


Figure 27
Dionchus agassizi: (**A**) ventral view. Scale: 0.5 mm; (**B**) hamulus. Scale: 0.05 mm. Drawn from USNM 35676.

24(23) Haptor with 14 muscular peduncles, each containing a marginal hook, cuticular ridges absent; anterior adhesive area with 4 pairs of head organs. Parasitic on the bluntnose stingray, *Dasyatis say.* ..... ***Loimopapillosum dasyatis* (Fig. 28)**

24(23) Haptor lacking peduncles, cuticular ridges present on dorsal surface; anterior adhesive area consisting of 2 or 4 small preoral suckers in a transverse row. Parasitic on requiem sharks (Carcharhinidae). ..... ***Loimos* spp. (Fig. 29)**

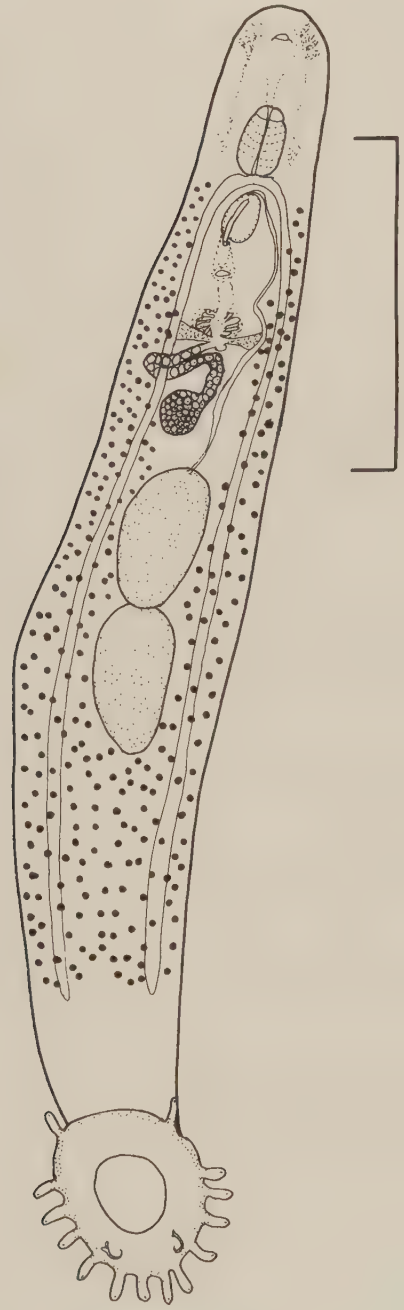


Figure 28
Loimopapillosum dasyatis: ventral view. Scale: 0.5 mm. Drawn from USNM 38145.

Figure 29
Loimos salpinggoides: (**A**) ventral view. Scale: 0.5 mm; (**B**) hamulus. Drawn from USNM 35675.

25(5) Testis 1, male copulatory apparatus unarmed. Parasitic on spiny dogfish and dusky sharks, *Carcharhinus obscurus*. ..... ***Microbothrium apiculatum*** **(Fig. 30)**

25(5) Testes 2 or more, male copulatory apparatus armed with spines..... **26**

Figure 30
Microbothrium apiculatum: ventral view. Scale: 1 mm. Drawn from USNM 35684.

26(25) Testes 2, opposite, male copulatory apparatus with 2 rows of about 25 long riblike spines in the thicker anteroventral wall and 1 row of about 30 short straight spines on the posterodorsal wall. Parasitic on requiem sharks (Carcharhinidae). ..... ***Dermophthirius*** **spp. (Fig. 31)**

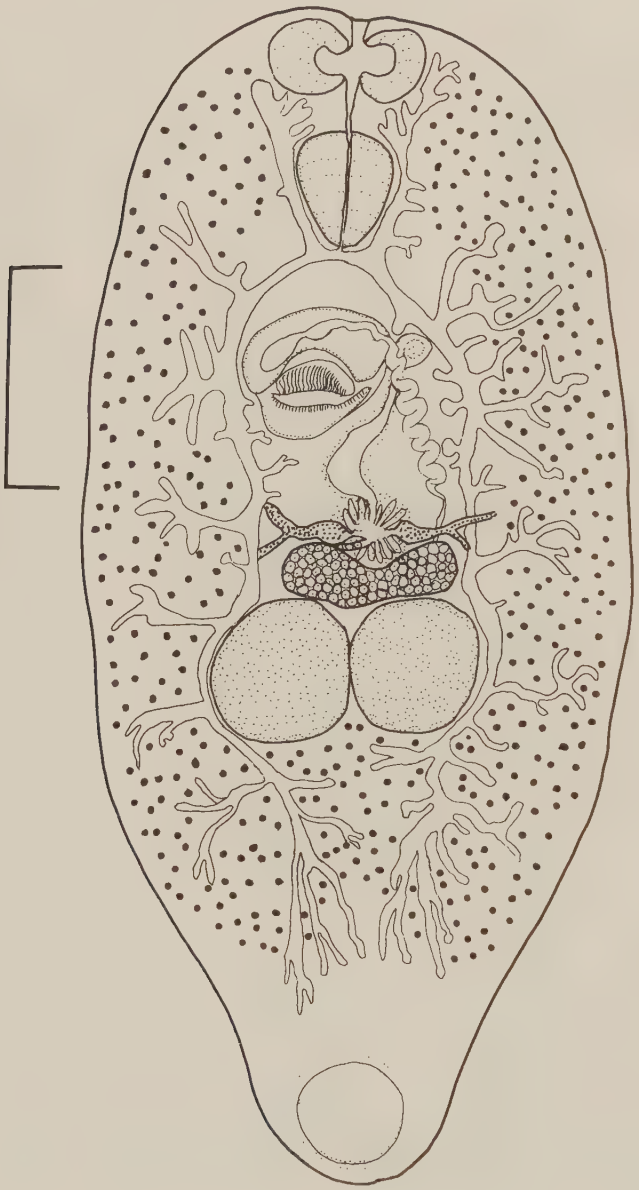


Figure 31
Dermophthirius carcharhini: ventral view. Scale: 0.5 mm. Drawn from USNM 35687.

26(25) Testes several, male copulatory apparatus with a row of large simple recurved spines and several rows of small straight spines on its ventral surface. Parasitic on lemon shark, *Negaprion brevirostris*. . . . . ***Neodermophthirius harkemai*** **(Fig. 32)**

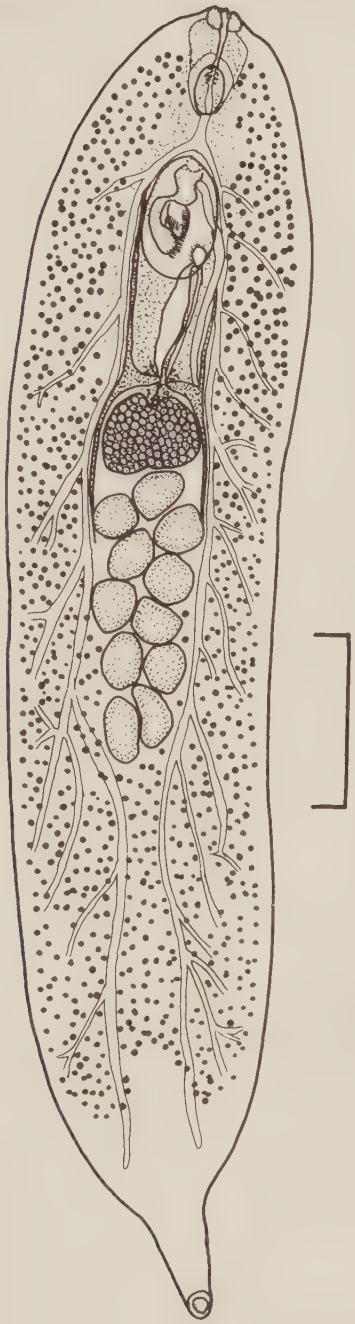


Figure 32
Neodermophthirius harkemai: ventral view. Scale: 1 mm. Drawn from USNM 37751.

27(3) Viviparous (embryo may be visible in uterus); haptor with 16 marginal hooks and 1 pair of hamuli; eyespots absent; vitellaria poorly developed. Parasitic on killifishes (Cyprinodontidae) and sticklebacks (Gasterosteidae)..... **(Family Gyrodactylidae) 28**

27(3) Oviparous; haptor with 14 marginal hooks and 2 pairs of hamuli; eyespots present; vitellaria extensive..... **30**

28(27) Haptor with deep transverse bar absent, lateral winglike processes present, pitted peduncular bar present just anterior to haptor. Parasitic on *Fundulus* spp..... ***Swingleus* sp. (Fig. 33)**

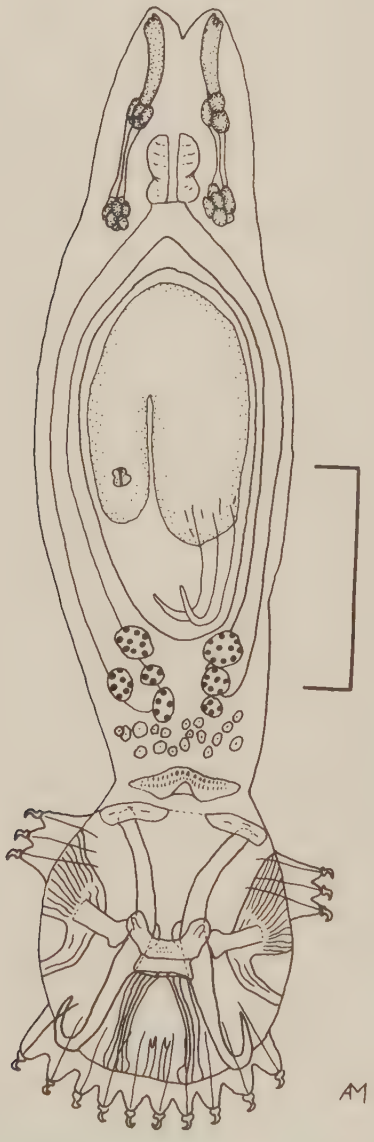


Figure 33
Swingleus polyclithroides: ventral view. Scale: 0.1 mm. Drawn from USNM 72511.

28(27) Haptor with deep transverse bar present, lateral winglike processes absent, peduncular bar present or absent. **29**

29(28) Peduncular bar large, present on ventral surface just anterior to haptor. Parasitic on cyprinodonts. . . . . ***Fundulotrema prolongis*** **(Fig. 34)**

29(28) Peduncular bar absent. Parasitic on cyprinodonts and sticklebacks. . . . . ***Gyrodactylus stephanus*** **(Fig. 35)**

30(27) Haptor with 3 transverse bars; posterior of body with spines. Parasitic on drums (Sciaenidae). . . . . **(Family Diplectanidae) 31**

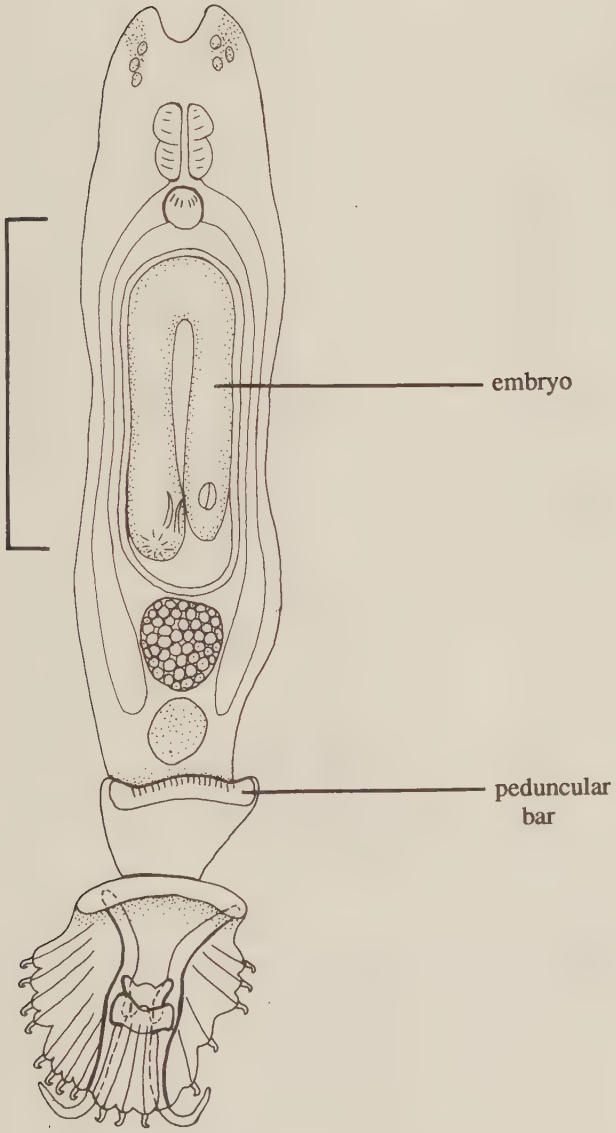


Figure 34
Fundulotrema prolongis: ventral view. Scale: 0.1 mm. Drawn from USNM 49331.

Figure 35
Gyrodactylus stephanus: ventral view. Scale: 0.1 mm. Drawn from USNM 49332.

30(27) Haptor with 0, 1, or 2 transverse bars; posterior of body lacking spines. **32**

31(30) Haptor with dorsal and ventral squamodisks composed of scalelike spines; rows of accessory hooklike spines on posterior of body absent. Parasitic on spotted seatrout, *Cynoscion nebulosus.* . . . . . ***Diplectanum bilobatum* (Fig. 36)**

31(30) Haptor lacking squamodisks; bilateral patches or rows of accessory hooklike spines present on posterior body. Parasitic on sciaenids. . . . . ***Rhamnocercus* spp. (Fig. 37)**

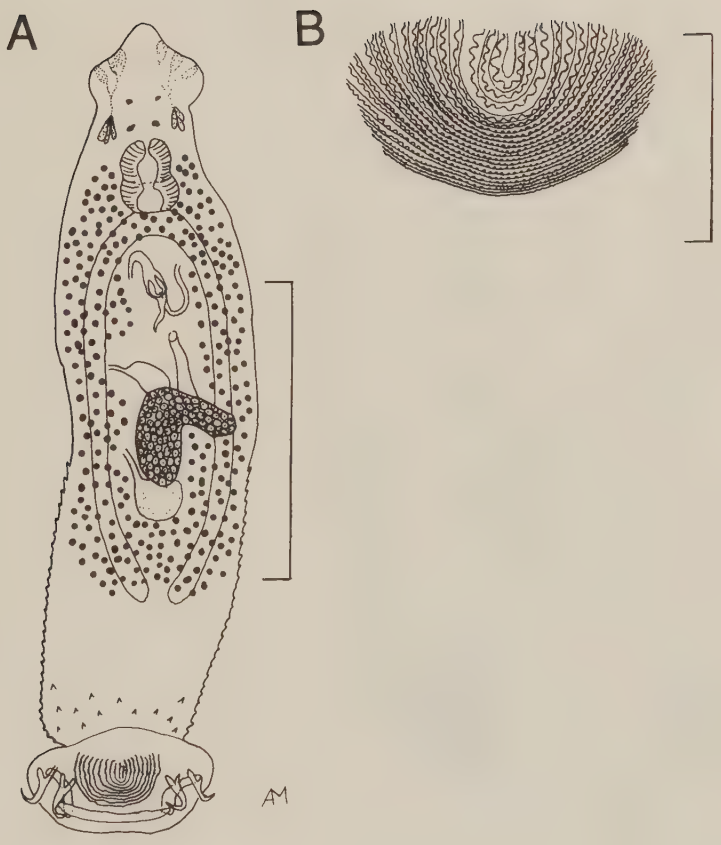


Figure 36
Diplectanum bilobatum: (**A**) ventral view. Scale: 0.2 mm; (**B**) ventral squamodisk. Scale: 0.05 mm. Drawn from USNM 39364.

Figure 37
Rhamnocercus bairdiella: ventral view. Scale: 0.2 mm. Drawn from USNM 49345.

32(30) Haptor bilobed, with peduncles, transverse bars absent. Parasitic on Atlantic torpedo, *Torpedo nobiliana*. . . . . ***Amphibdella flavolineata* (Fig. 38)**

32(30) Haptor with 1 or 2 transverse bars. **33**

33(32) Haptor with 1 transverse bar. **34**

33(32) Haptor with 2 transverse bars. **35**

Figure 38
Amphibdella flavolineata: (**A**) ventral view. Scale: 1 mm; (**B**) hamulus. Drawn from USNM 35159.

34(33) Haptor broadly bilobed; eyespots present. Parasitic on smooth flounder, *Pleuronectes putnami.* ..... ***Protancyrocephaloides liopsettae*** **(Fig. 39)**

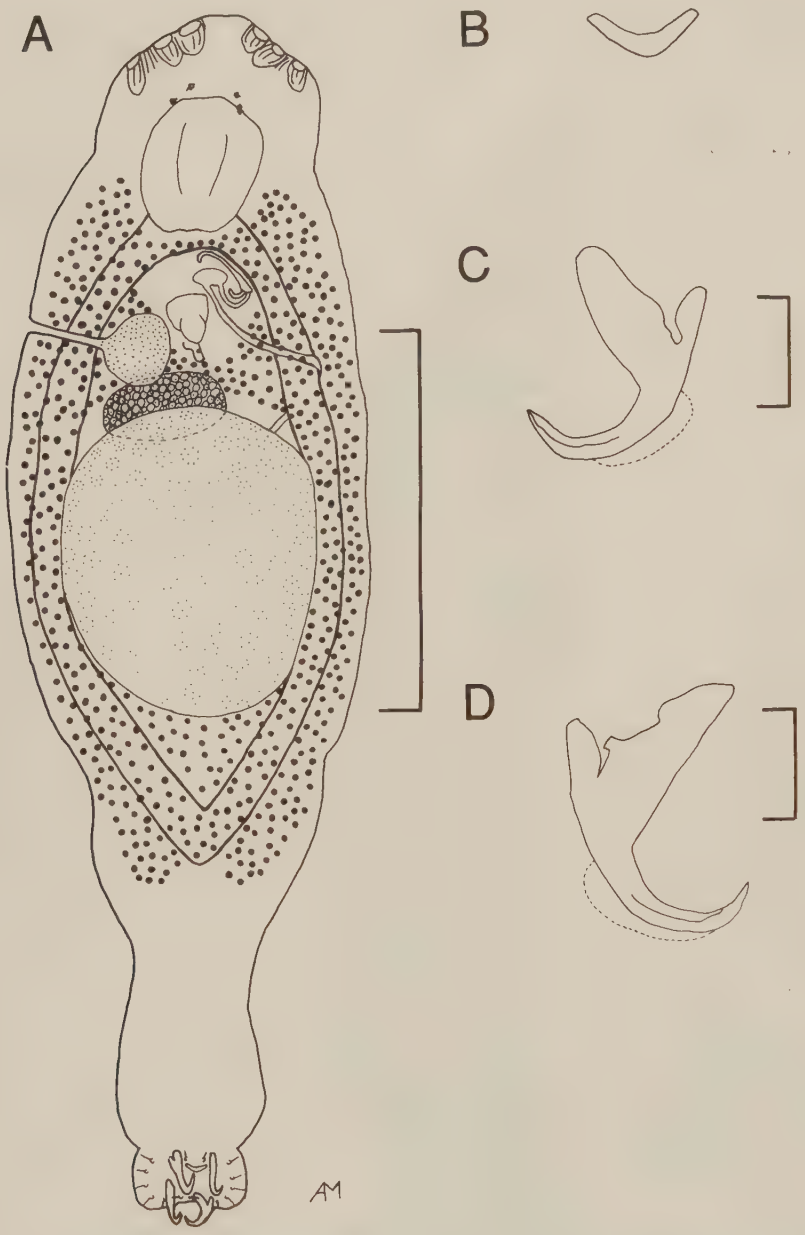


Figure 39

Protancyrocephaloides liopsettae. (**A**) ventral view. Scale: 0.5 mm; (**B**) transverse bar; (**C**) ventral hamulus; (**D**) dorsal hamulus. B–D scales: 0.05 mm. Drawn from USNM 74609.

34(33) Haptor entire; eyespots absent. Parasitic on spiny dogfish and Atlantic torpedo. ..... ***Amphibdelloides maccallumi*** **(Fig. 40)**

35(33) Haptor with radially arranged row of troughlike sclerotized supporting structures. Parasitic on windowpane, *Scophthalmus aquosus.* ..... ***Bothitrema bothi*** **(Fig. 41)**

35(33) Haptor lacking radially arranged sclerotized supporting structures. **36**

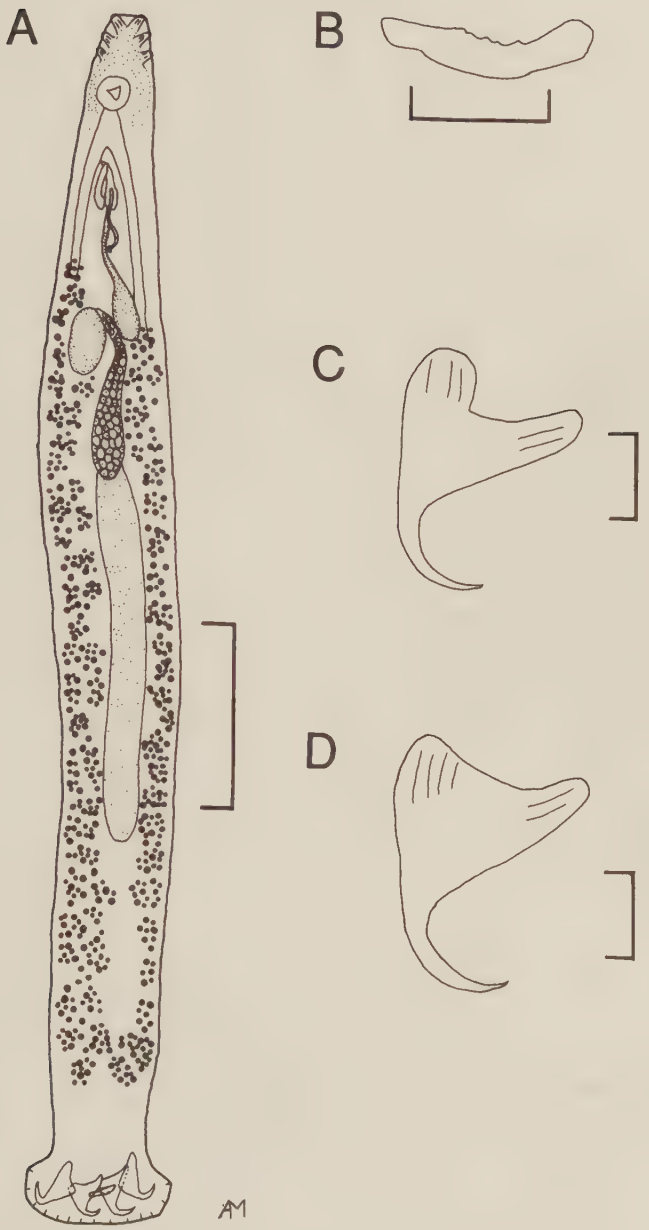


Figure 40
Amphibdelloides maccallumi: (**A**) ventral view. Scale: 0.5 mm; (**B**) ventral bar; (**C**) ventral hamulus; (**D**) dorsal hamulus. B–D scales: 0.05 mm. Drawn from USNM 35700.

Figure 41
Bothitrema bothi: ventral view. Scale: 0.5 mm. Drawn from specimens collected from windowpane, *Scophthalmus aquosus,* off New Jersey.

36(35) Intestinal ceca not confluent posteriorly; body much broader than haptor; male copulatory apparatus contains a thin fishhook-shaped sclerotized penis with a thin elongate Y-shaped accessory piece. Parasitic on Atlantic needlefish, *Strongylura marina*..... ***Ancyrocephalus parvus*** **(Fig. 42)**

36(35) Intestinal ceca confluent posteriorly; body about as broad as haptor..... **37**

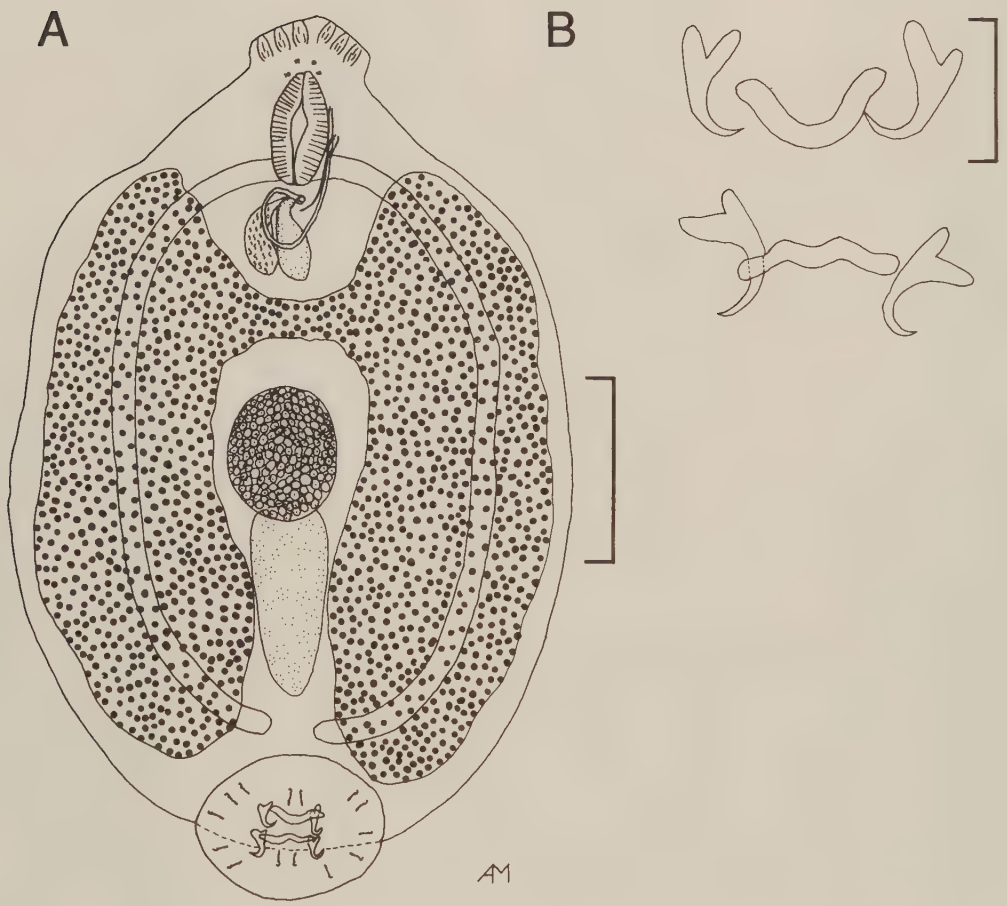


Figure 42

Ancyrocephalus parvus: (**A**) ventral view. Scale: 0.2 mm; (**B**) hamuli and transverse bars. Scale: 0.025 mm. Drawn from USNM 8143.

37(36) Haptor dorsal transverse bar with knobbed lateral extremities; penis sclerotized, tubular, straight, with spiral thread and Y-shaped accessory piece. Parasitic on white perch, *Morone americana*. ..... ***Onchocleidus nactus*** **(Fig. 43)**

37(36) Haptor dorsal transverse bar without lateral knobs; penis tube curved, without spiral thread..... **38**

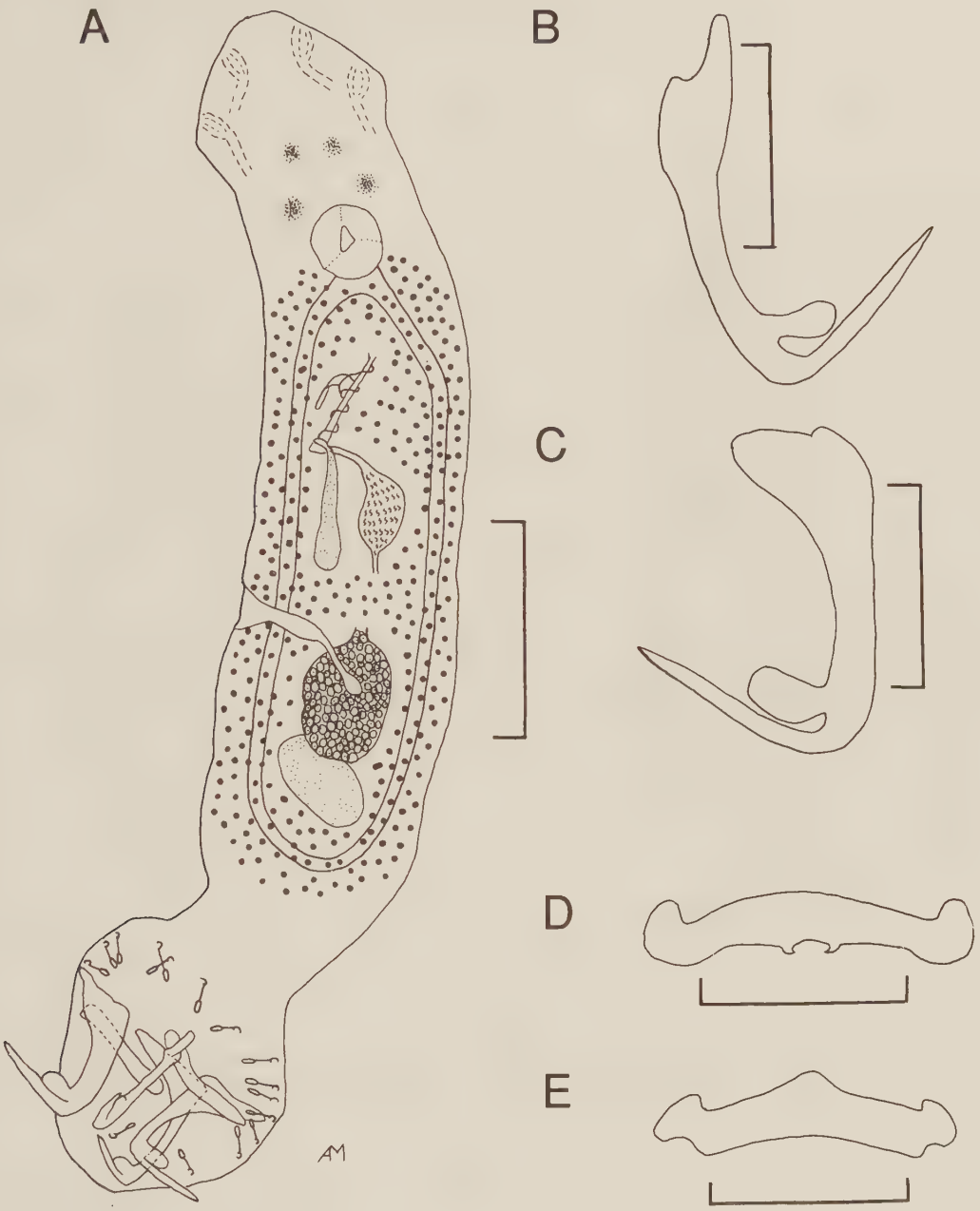


Figure 43

Onchocleidus nactus: (**A**) ventral view. Scale: 0.05 mm; (**B**) dorsal hamulus; (**C**) ventral hamulus; (**D**) dorsal bar; (**E**) ventral bar. B–D scales: 0.02 mm. Drawn from USNM 73744.

38(37) Haptor ventral transverse bar bifid laterally, lacking prominent sculpturing. Parasitic on Atlantic spadefish, *Chaetodipterus faber*..... ***Pseudohaliotrema longiphallus*** **(Fig. 44)**

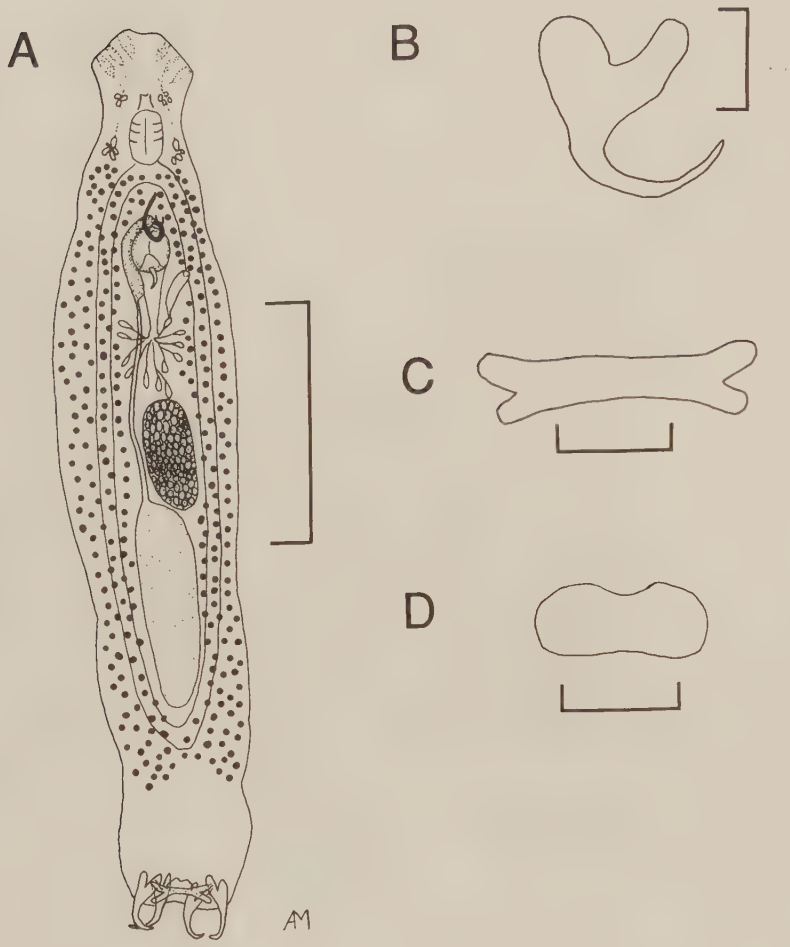


Figure 44

Pseudohaliotrema longiphallus: (**A**) ventral view. Scale: 0.2 mm; (**B**) ventral hamulus; (**C**) ventral transverse bar; (**D**) dorsal transverse bar. B–D scales: 0.025 mm. Drawn from USNM 36959.

38(37) Haptor ventral transverse bar rounded laterally, with prominent medial sculpturing. Parasitic on striped mullet, *Mugil cephalus*. ..... ***Haliotrema vanbenedeni*** **(Fig. 45)**

39(1) Haptor with 4 or more clamps, posterior haptoral appendix present or absent; anterior adhesive area a pair of buccal suckers. **44**

39(1) Haptor with 3 pairs of suckers, each having a curved hooklike sclerite; posterior haptoral appendix present; anterior adhesive area an oral sucker or shallow muscular grooves. **40**

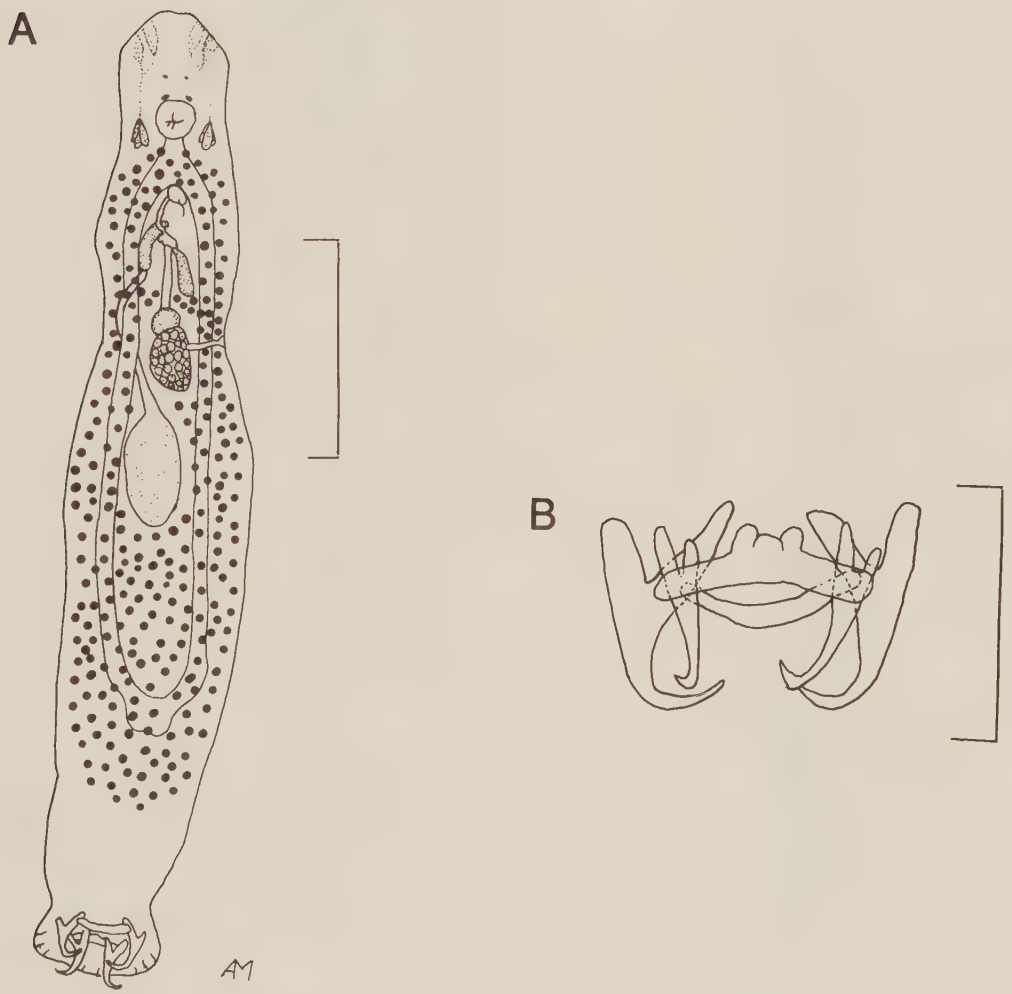


Figure 45

Haliotrema vanbenedeni: (**A**) dorsal view. Scale: 0.2 mm; (**B**) hamuli and transverse bars. Scale: 0.05 mm. Drawn from USNM 49342.

40(39) Haptoral appendix armed with 3 pairs of sclerites and 1 pair of small suckers; mouth flanked by 1 pair of ventral muscular depressions; 2 pairs of eyespots present. Parasitic on shortnose sturgeon, *Acipenser brevirostrum*. . . . . ***Diclybothrium armatum*** **(Fig. 46)**

40(39) Haptoral appendix with 1 pair of small hamuli and 1 pair of distinctly muscular suckers; anterior adhesive area an oral sucker; eyespots absent. Parasitic on elasmobranchs.
. . . . . **(Family Hexabothriidae) 41**

Figure 46
Diclybothrium armatum: (**A**) ventral view. Scale: 2 mm; (**B**) haptoral appendix. Scale: 0.2 mm. Drawn from USNM 73136.

41(40) Male copulatory complex armed with small curved spines; eggs with filamentous appendage at abopercular pole. Parasitic on smooth dogfish, *Mustelus canis*. . . . . ***Hexabothrium musteli*** **(Fig. 47)**

41(40) Male copulatory complex unarmed; eggs with or without 2 polar appendages **42**

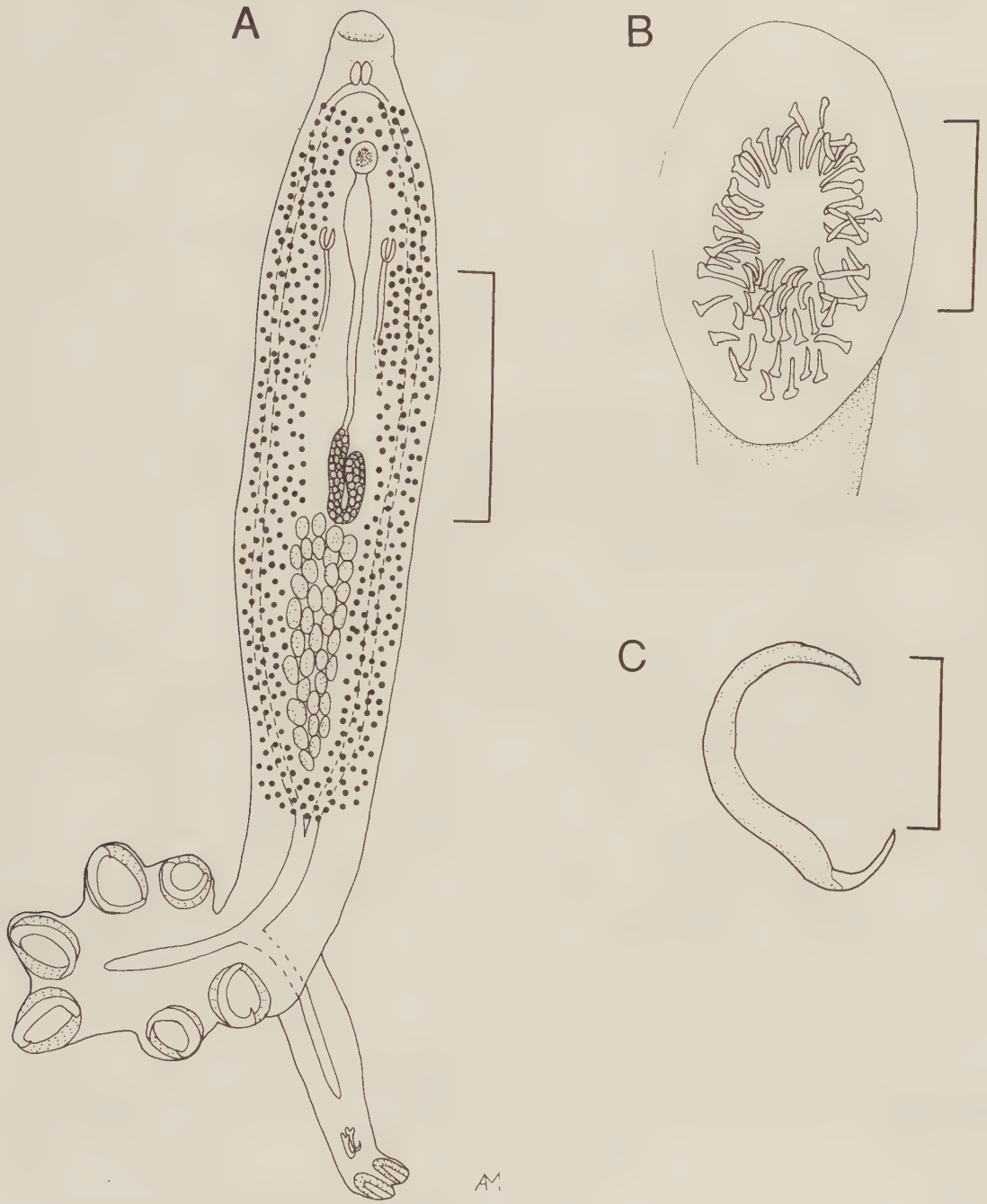


Figure 47

Hexabothrium musteli: (**A**) ventral view. Scale: 0.5 mm; (**B**) cirrus. Scale: 0.05 mm; (**C**) sucker sclerite. Scale: 0.1 mm. Drawn from USNM 8132.

42(41) Vaginae merge to form a single duct before entering vitelline reservoir; ovary proximally lobate, descending and ascending branches sinuous; eggs with ridges, lacking elongate polar appendages. Parasitic on the barndoor skate, *Raja laevis*. ..... ***Rajonchocotyle laevis*** **(Fig. 48)**

42(41) Vaginae do not merge, enter transverse vitelline duct separately; ovary proximally branched; eggs lacking ridges, with 2 elongate polar appendages. Parasitic on sharks or spiny dogfish. **43**

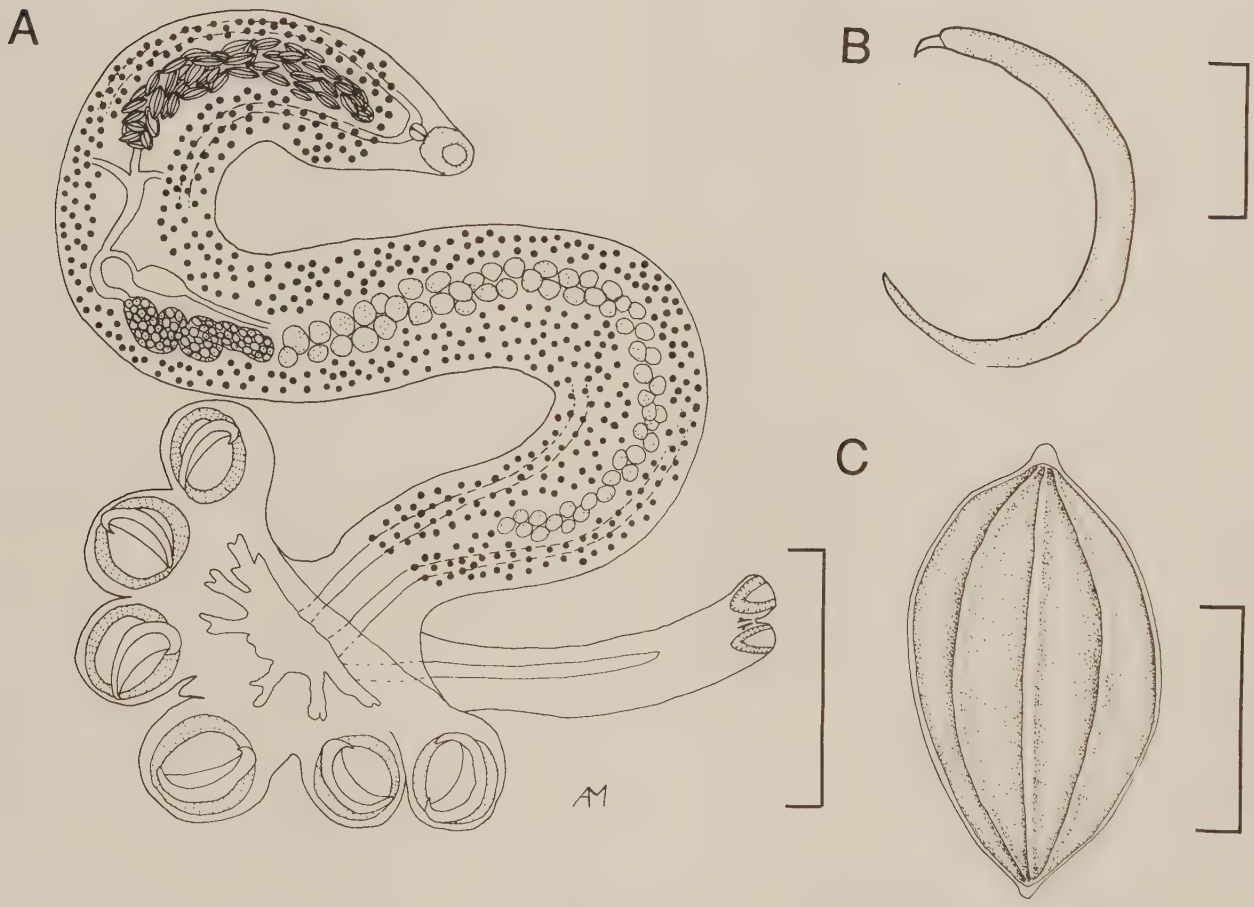


Figure 48

Rajonchocotyle laevis: (**A**) ventral view. Scale: 2 mm; (**B**) sclerite. Scale: 0.5 mm; (**C**) egg. Scale 0.1 mm. Drawn from USNM 36721.

43(42) Descending branch of ovary straight; ootype smooth. Parasitic on requiem sharks (Carcharhinidae) and hammerhead sharks (Sphyrnidae). ..... ***Erpocotyle* spp. (Fig. 49)**

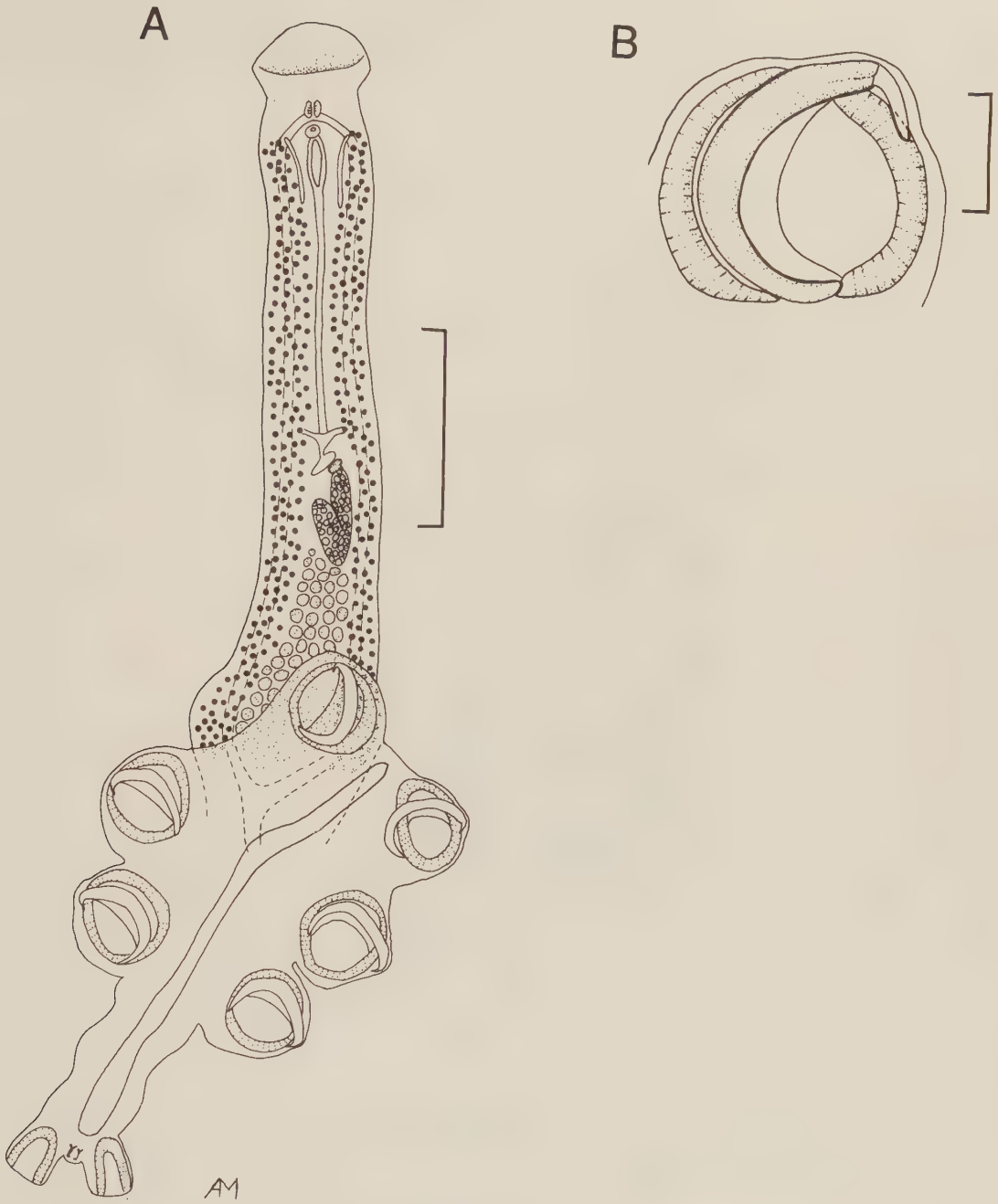


Figure 49

Erpocotyle sphyrnae: (**A**) ventral view. Scale: 1 mm; (**B**) sucker with sclerite. Scale: 0.2 mm. Drawn from USNM 8136.

43(42) Descending branch of ovary sinuous; ootype with longitudinal row of large cells giving ribbed appearance. Parasitic on spiny dogfish..... ***Squalonchocotyle*** **spp. (Fig. 50)**

Figure 50
Squalonchocotyle squali: (**A**) ventral view. Scale: 1 mm; (**B**) sclerite. Scale: 0.1 mm. Drawn from USNM 8133.

44(39) Haptor with 4 clamps, terminal lappet broad. Parasitic on jacks (*Caranx* spp.). ..... ***Protomicrocotyle mirabilis* (Fig. 51)**

44(39) Haptor with more than 4 clamps. **45**

45(44) Haptor with 5 to 8 clamps. **46**

45(44) Haptor with more than 8 clamps. **63**

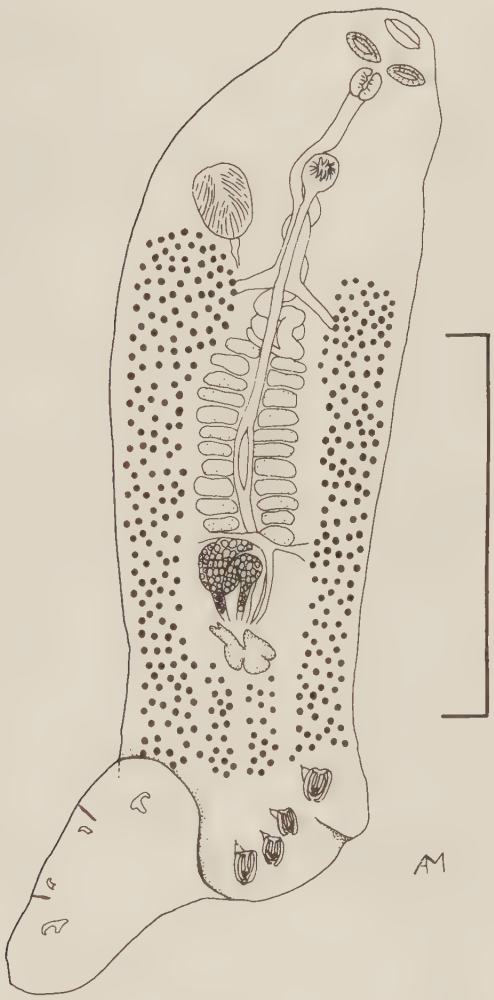


Figure 51
Protomicrocotyle mirabilis: ventral view. Scale: 0.5 mm. Drawn from USNM 37110.

46(45) Clamps with a patch of approximately 30 spines in the outer anterior quadrant, 8 sclerites on each asymmetric clamp. Parasitic on pollock, *Pollachius virens*. . . . . ***Diclidophora denticulata*** **(Fig. 52)**

46(45) Clamps without spines. **47**

47(46) Clamps approximately equal in size, with muscular sucker in one quadrant. **48**

47(46) Clamps unequal in size, without muscular sucker. **51**

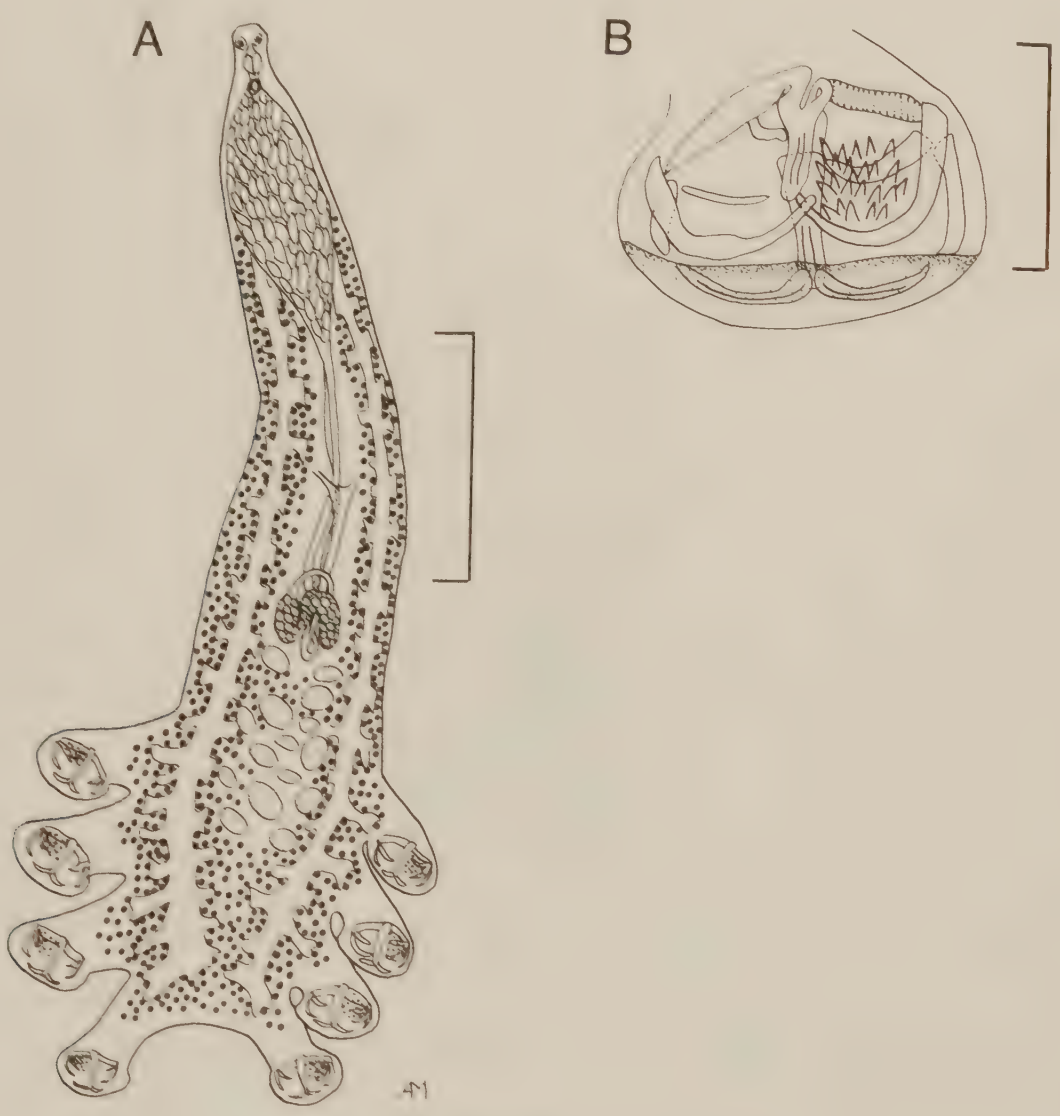


Figure 52
Diclidophora denticulata: (**A**) ventral view. Scale: 2 mm; (**B**) clamp. Scale: 0.4 mm. Drawn from USNM 63394.

48(47) Body constricted to form prehaptoral peduncle; vitelline follicles absent in peduncle. Parasitic on summer flounder, *Paralichthys dentatus*, and seatrout, *Cynoscion* spp. . . . . ***Neoheterobothrium* spp. (Fig. 53)**

48(47) Body not constricted to form prehaptoral peduncle; vitelline follicles extend to or into haptor. **49**

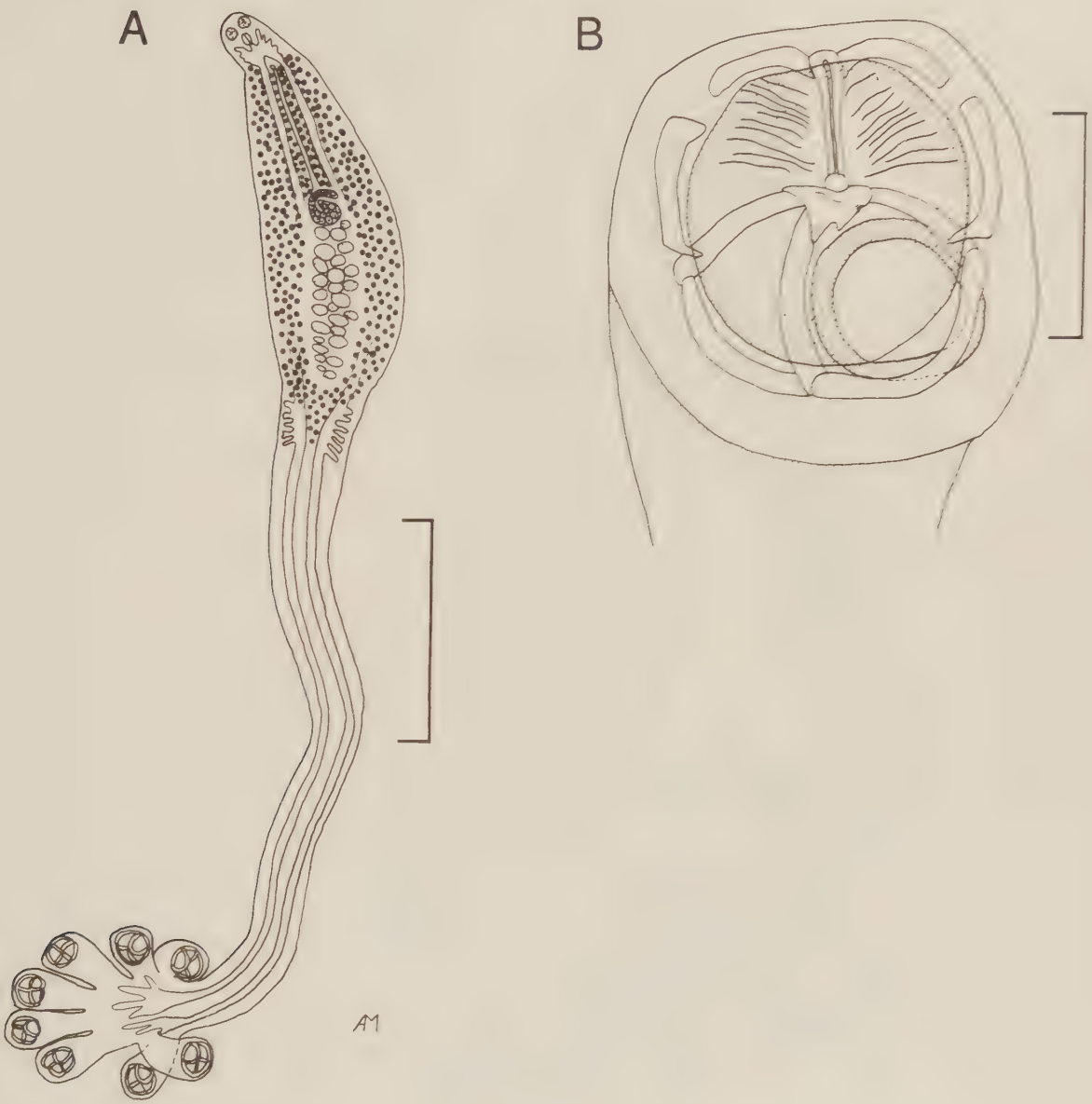


Figure 53
Neoheterobothrium affine. (**A**) ventral view. Scale: 2 mm; (**B**) clamp. Scale: 0.2 mm. Drawn from USNM 4676.

49(48) Haptor with 3 pairs of pedunculate clamps and 1 pair of small sessile clamps at the posterior of the haptoral appendix. Parasitic on silver perch, *Bairdiella chrysoura*, and white perch. . . . ***Pedocotyle* spp. (Fig. 54)**

49(48) Haptor with 4 pairs of pedunculate clamps; haptoral appendix and sessile clamps absent. **50**

Figure 54
Pedocotyle morone: (**A**) ventral view. Scale: 2 mm; (**B**) pedunculate clamp. Scale: 0.2 mm. Drawn from USNM 35594.

50(49) Testes postovarian; seminal receptacle preovarian; vitelline follicles extend to but do not enter haptor. Parasitic on pigfish, *Orthopristis chrysoptera*, and northern kingfish, *Menticirrhus saxatilis*. ..... ***Choricotyle* spp. (Fig. 55)**

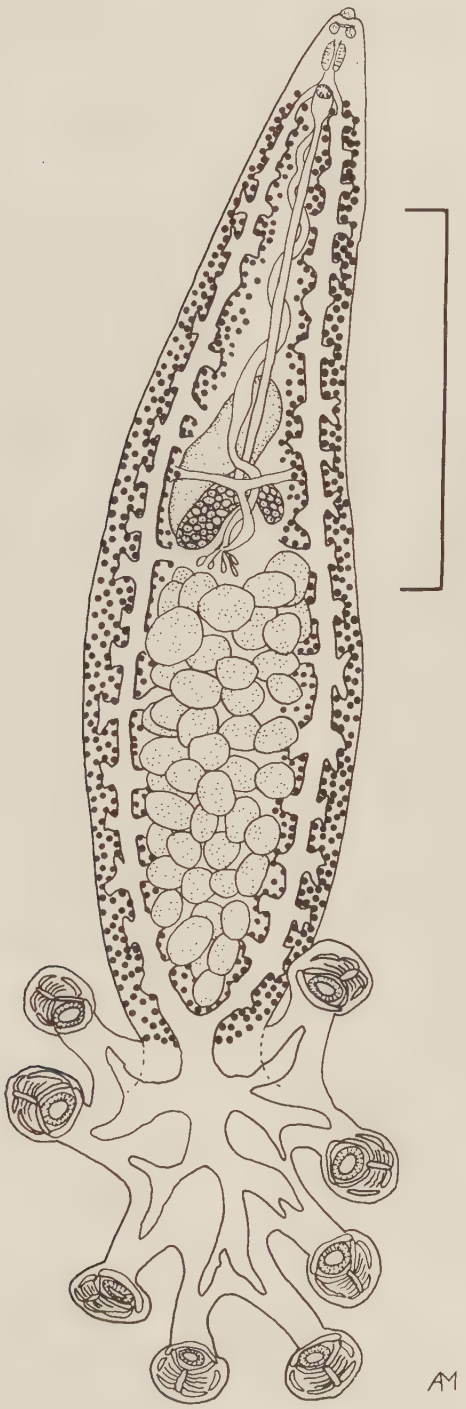


Figure 55
Choricotyle aspinachorda, ventral view. Scale: 2 mm. Drawn from USNM 38151.

50(49) Testes and seminal receptacle both postovarian; vitelline follicles extend into the haptor. Parasitic on searobins, *Prionotus* spp. ..... ***Orbocotyle prionoti* (Fig. 56)**

51(47) Clamps pedunculate, with 8 sclerites. **52**

51(47) Clamps pedunculate or sessile, fewer than 8 sclerites. **53**

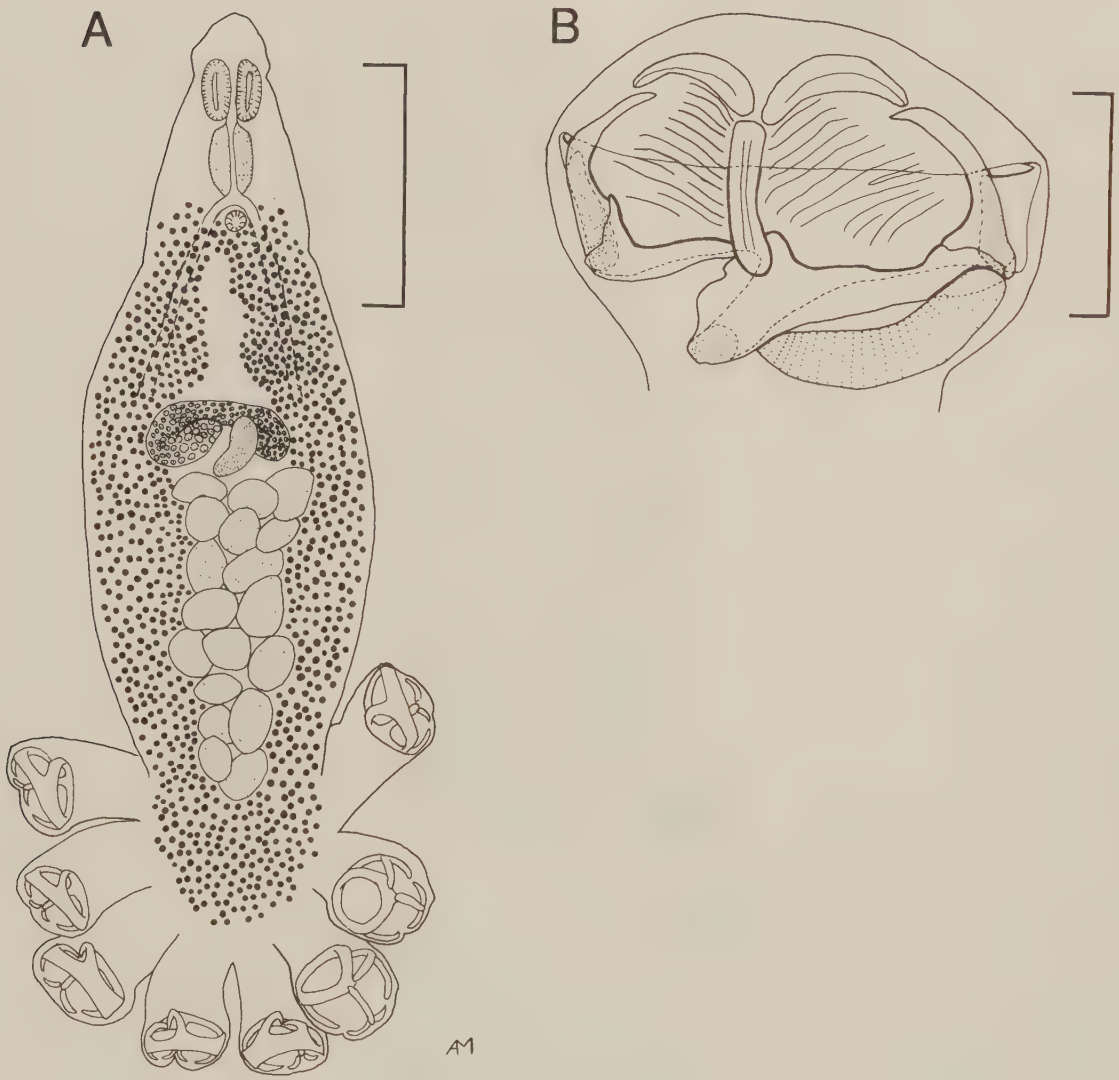


Figure 56

Orbocotyle prionoti: (**A**) ventral view. Scale: 0.5 mm; (**B**) pedunculate clamp. Scale: 0.1 mm. Drawn from specimens collected from northern searobins, *Prionotus carolinus,* in the New York Bight.

52(51) Clamps progressively larger towards posterior of haptor. Parasitic on hakes (Gadidae).
. . . . . ***Diclidophoroides maccallumi*** **(Fig. 57)**

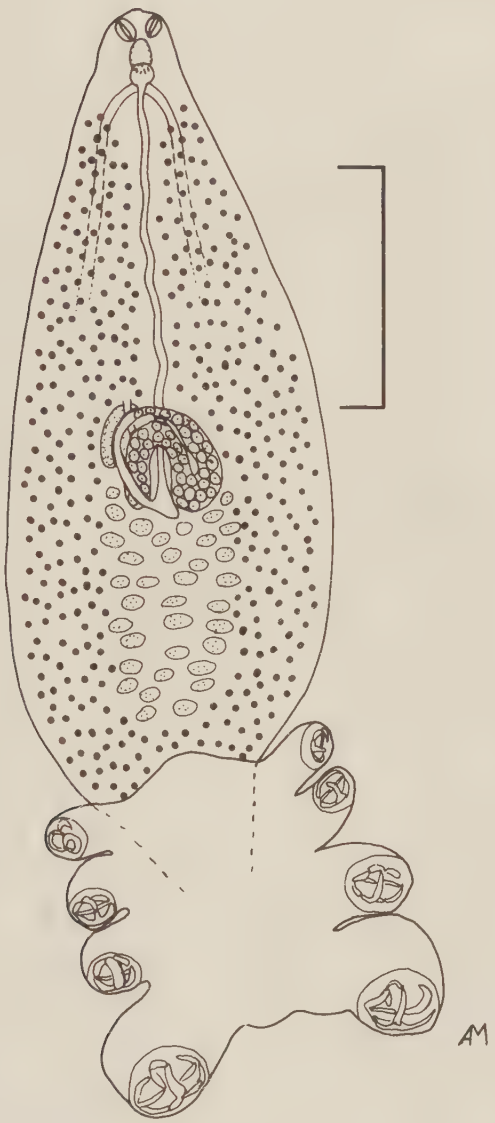


Figure 57
Diclidophoroides maccallumi: ventral view. Scale: 2 mm. Drawn from USNM 35106.

52(51) Clamps progressively smaller towards posterior of haptor. Parasitic on Atlantic croaker, *Micropogonias undulatus*. . . . . ***Absonifibula bychowskyi*** **(Fig. 58)**

53(51) Suckerlike muscular clamps with 3 sclerites, the middle one X-shaped. Parasitic on scombrids. . . . . **(Family Hexostomatidae) 54**

53(51) Clamps with more than 3 sclerites, none X-shaped. **55**

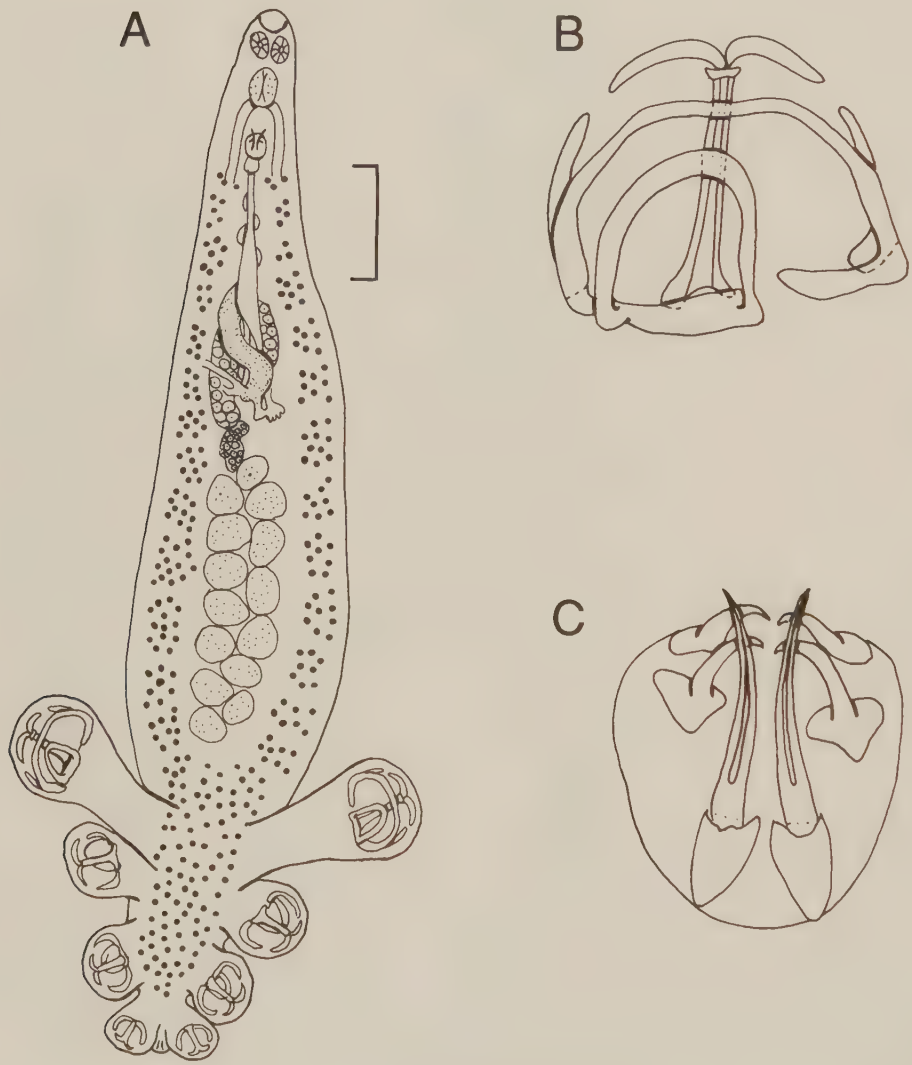


Figure 58
Absonifibula bychowskyi: (**A**) ventral view. Scale: 0.3 mm; (**B**) clamp; (**C**) cirrus spines. Drawn from USNM 73245.

54(53) Haptor with 4 pairs of sessile clamps in 2 longitudinal rows, the posterior pair slightly smaller than the others. Parasitic on little tunny..... ***Neohexostoma euthynni*** **(Fig. 59)**

Figure 59

Neohexostoma euthynni: (**A**) ventral view. Scale: 1 mm; (**B**) sessile clamp. Scale: 0.2 mm. Drawn from USNM 74151.

54(53) Haptor with 4 pairs of sessile clamps in a transverse row along posterior margin, median pair about one-half the size of the others. Parasitic on Atlantic bonito, *Sarda sarda* . . . . . ***Hexostoma lintoni* (Fig. 60)**

55(53) Clamps sessile, anterior pair much larger than posterior 3 pairs, terminal lappet with 1 pair of hamuli and 2 pairs of marginal hooks of which 1 pair is enlarged. Parasitic on hakes (*Merluccius* spp.). . . . . ***Anthocotyle merluccii* (Fig. 61)**

55(53) Clamps sessile, anterior pair not larger than posterior 3 pairs. **56**

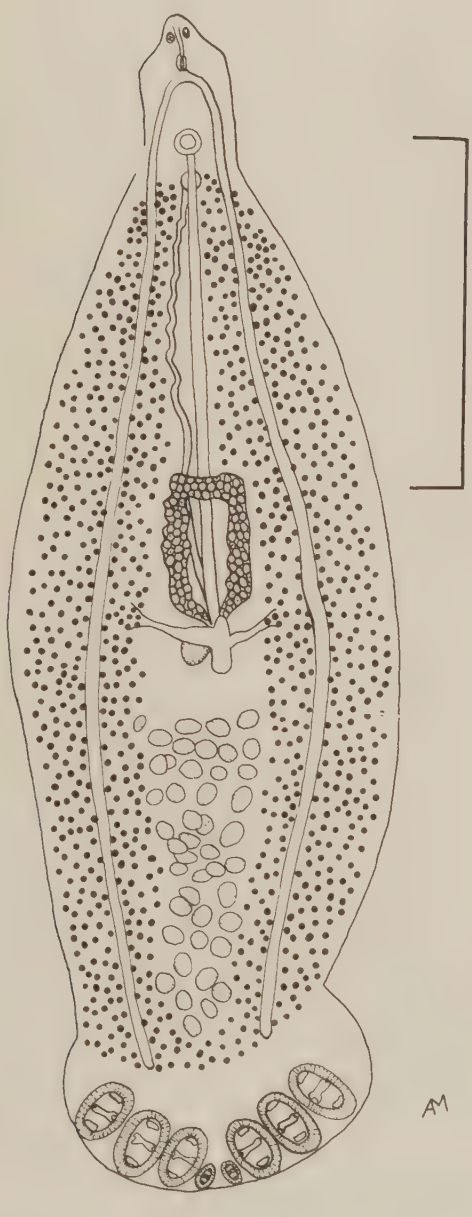
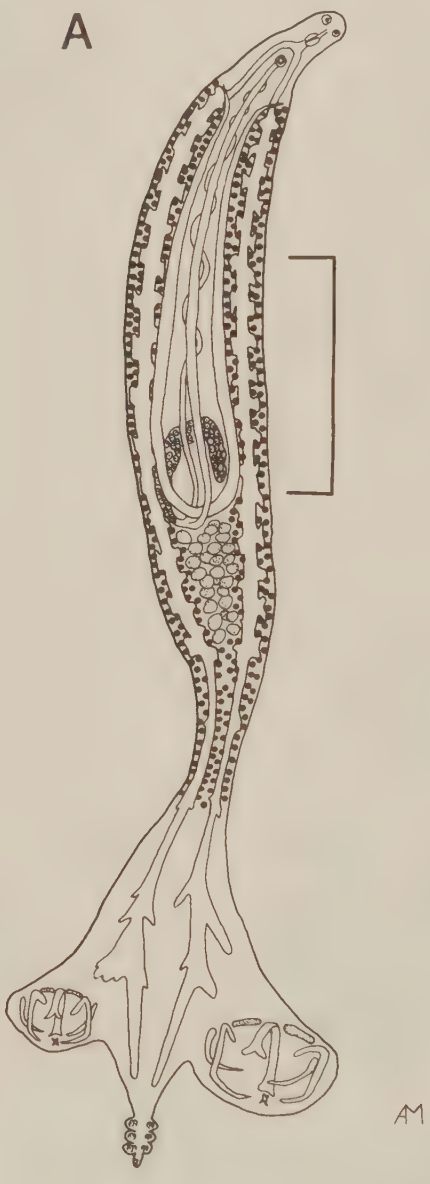


Figure 60
Hexostoma lintoni: ventral view. Scale: 2 mm. Drawn from USNM 6676.



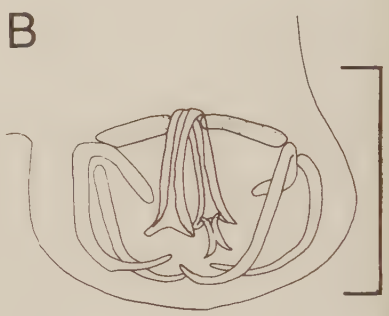


Figure 61
Anthocotyle merluccii: (**A**) ventral view. Scale: 2 mm; (**B**) large clamp. Scale: 1 mm. Drawn from USNM 35607.

56(55) Haptor divided by a deep cleft into 2 narrow lobes, each lobe with 4 clamps; 1 pair of small hamuli at the base of the cleft. Parasitic on Florida pompano, *Trachinotus carolinus*.
..... ***Bicotylophora trachinoti* (Fig. 62)**

56(55) Haptor not divided into 2 narrow lobes. **57**

57(56) Clamps approximately spherical, with 2 inverted U-shaped sclerites forming the anterior and posterior edges of the clamp opening; hamuli at the posterior margin of haptor; genital corona with 2 types of hooks. ..... **(Family Mazocraeidae) 58**

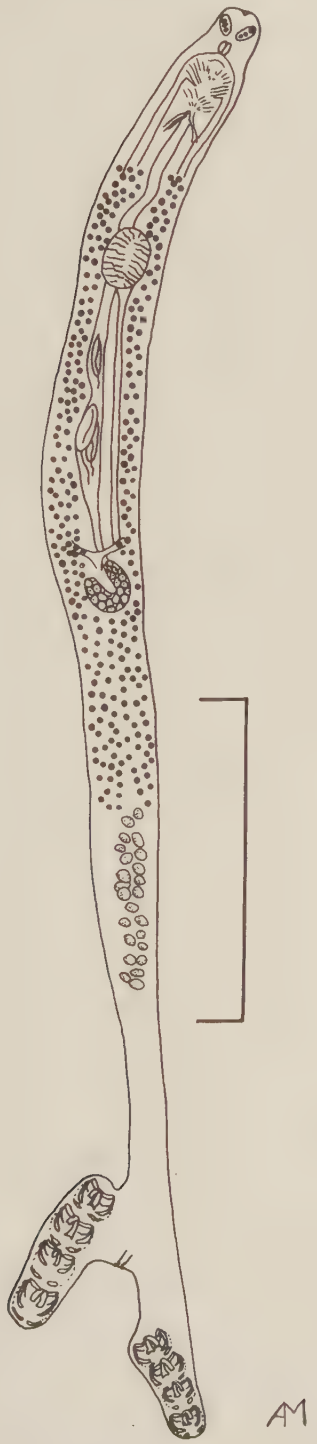


Figure 62
Bicotylophora trachinoti: ventral view. Scale: 1 mm. Drawn from USNM 35611.

57(56) Clamps elongated and usually modified in shape, U-shaped sclerites separated medially; 2 pairs of marginal hooks present at posterior margin of haptor; genital corona with a circle of curved hooks. ..... **(Family Macrovalvitrematidae) 61**

58(57) Haptor with 4 clamps on one side and 1 small clamp on the other. Parasitic on chub mackerel, *Scomber japonicus*. ..... ***Grubea cochlear* (Fig. 63)**

58(57) Haptor with 4 clamps on each side. **59**

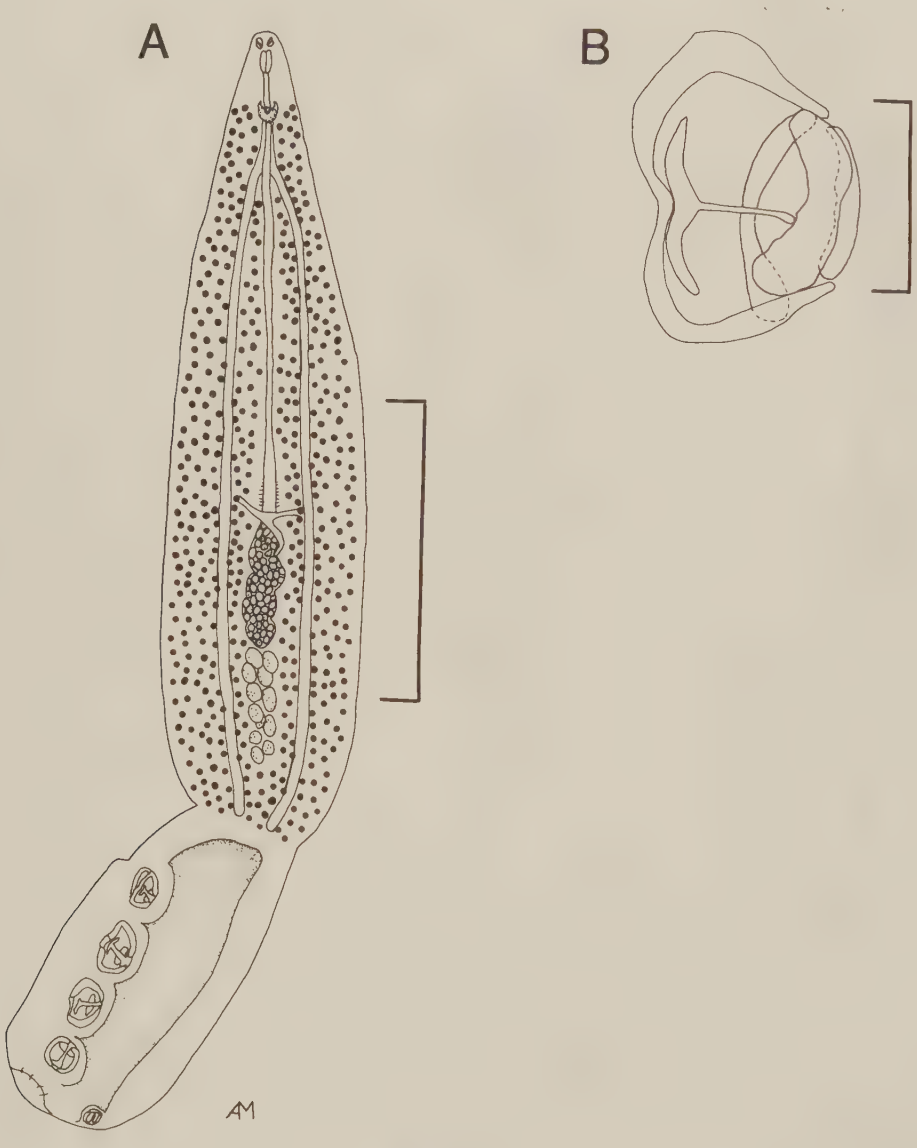


Figure 63
Grubea cochlear. (**A**) ventral view. Scale: 2 mm; (**B**) clamp. Scale: 0.2 mm. Drawn from USNM 8160.

59(58) Clamps on short, well-separated peduncules along the lateral margins of the body distributed anteriorly to the level of the gonads. Parasitic on herrings (Clupeidae). ..... ***Mazocraeoides*** **spp. (Fig. 64)**

59(58) Clamps confined to a distinct haptor. **60**

Figure 64
Mazocraeoides georgei: ventral view. Scale: 0.5 mm.
Drawn from USNM 35627.

60(59) Clamps pedunculate; haptoral lappet divided, with a pair of hamuli; vitellaria extend into haptor. Parasitic on Atlantic menhaden, *Brevoortia tyrannus*. . . . . ***Clupeocotyle brevoortia*** **(Fig. 65)**

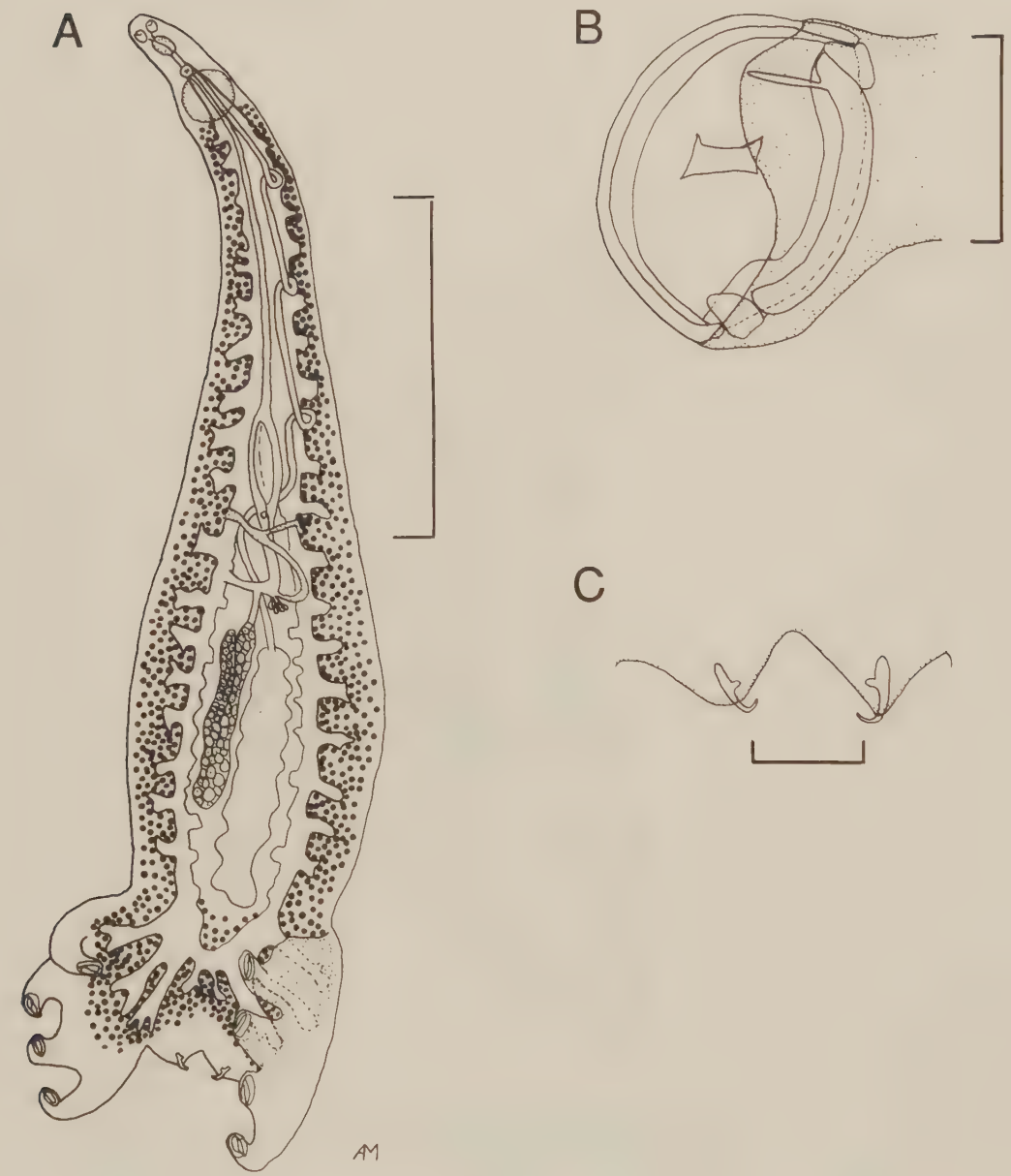


Figure 65
Clupeocotyle brevoortia: (**A**) ventral view. Scale: 1 mm; (**B**) clamp. Scale: 0.05 mm; (**C**) haptoral lappets. Scale: 0.1 mm. Drawn from USNM 37492.

60(59) Clamps sessile; haptoral lappet not divided, with a pair of hamuli; vitellaria extend to anterior margin of haptor. Parasitic on Atlantic mackerel, *Scomber scombrus*. . . . . ***Kuhnia scombri*** **(Fig. 66)**

61(57) Clamps dissimilar in shape, anterior 3 pairs of clamps an elongate "firetong" shape, posterior pair oblong; lateral margin of body behind the genital corona pleated; testis single. Parasitic on silver perch. . . . . ***Hargisia bairdiella*** **(Fig. 67)**

61(57) All clamps similar in shape; lateral body pleats absent; testes numerous. **62**

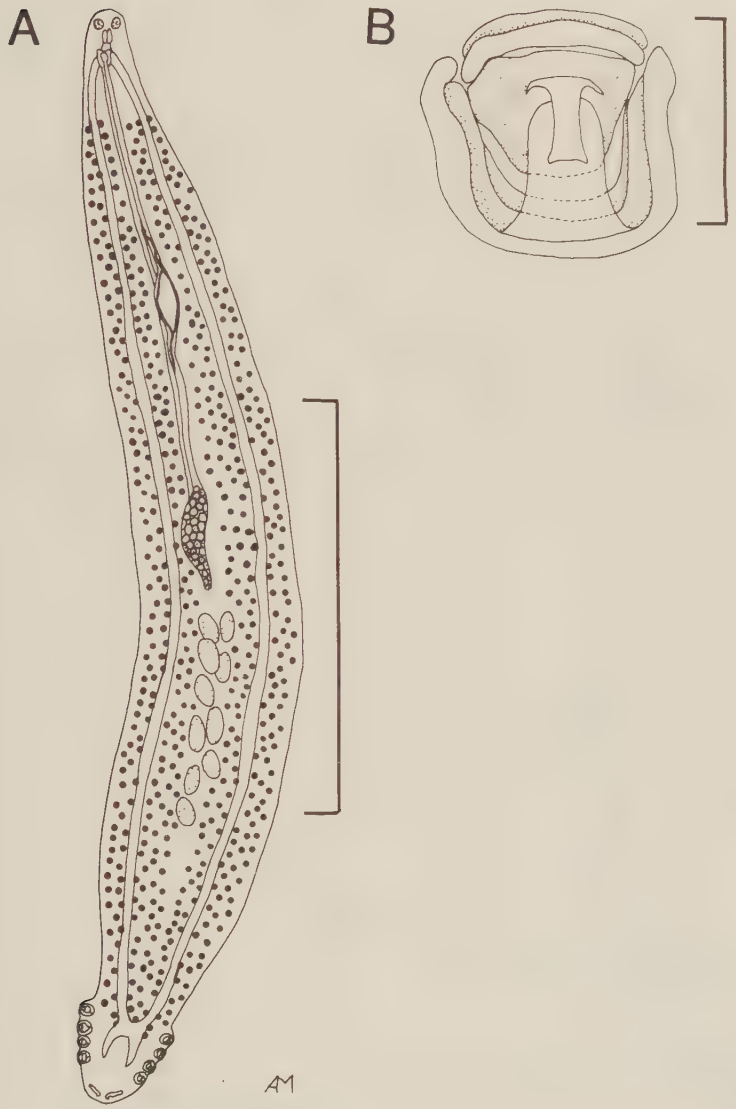


Figure 66
Kuhnia scombri: (**A**) ventral view. Scale: 2 mm; (**B**) clamp. Scale: 0.05 mm. Drawn from USNM 35620.

Figure 67
Hargisia bairdiella: ventral view. Scale: 0.1 mm. After Hargis, 1956a.

62(61) Clamp sclerites with toothlike serrations, anterior pair of clamps largest; genital corona with a circle of 6 to 7 small curved hooks. Parasitic on pigfish. ..... ***Pseudotagia cupida*** **(Fig. 68)**

62(61) Clamps sclerites lack toothlike serrations, posterior pair of clamps largest; genital corona with 10 to 12 curved hooks. Parasitic on Atlantic croaker. ..... ***Macrovalvitrematoides micropogoni*** **(Fig. 69)**

63(45) Haptor elongate, clamps in lateral rows on a distinct haptor or on side of body..... **67**

63(45) Haptor truncate or fishtail shaped, clamps in a row along posterior margin of haptor. **64**

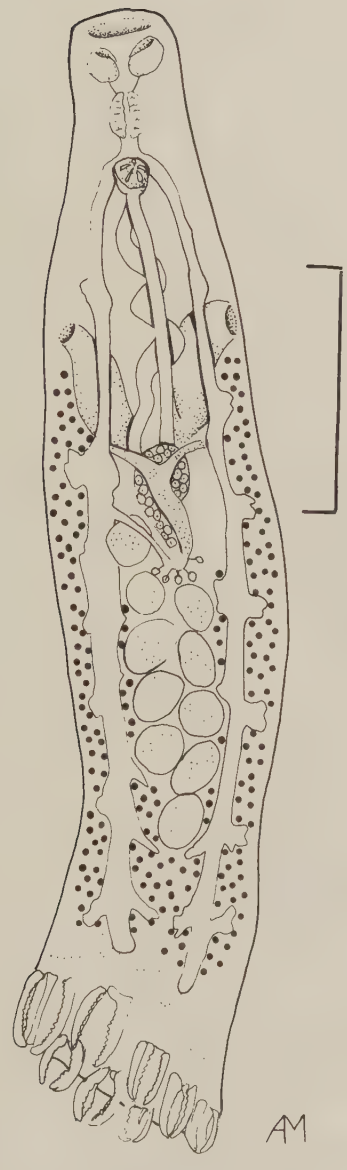


Figure 68
Pseudotagia cupida: ventral view. Scale: 0.3 mm. Drawn after Hargis, 1956a.

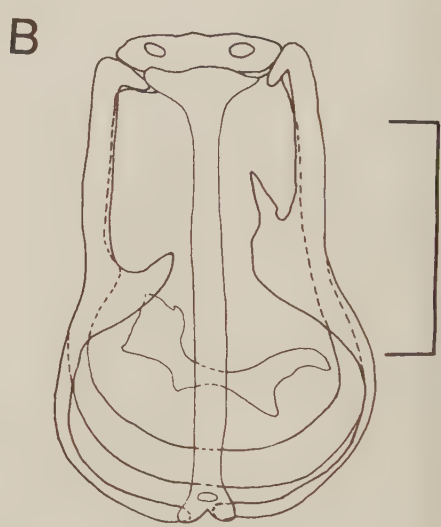


Figure 69
Macrovalvitrematoides micropogoni: (**A**) ventral view with clamps in lateral view. Scale: 0.2 mm; (**B**) clamp. Scale: 0.05 mm. Drawn from specimens collected from Atlantic croaker, *Micropogonias undulatus*, off Beaufort, North Carolina.

64(63) Haptor fishtail shaped, clamps of two different shapes, elongate "firetong" and ovoid microcotylid, on opposite lobes of haptor, hamuli absent. Parasitic on Florida pompano. ..... **(Family Pyragraphoridae)** ***Pyragraphorus pyragraphorus*** **(Fig. 70)**

64(63) Haptor truncate, clamps of one shape along posterior margin of haptor, hamuli present..... **65**

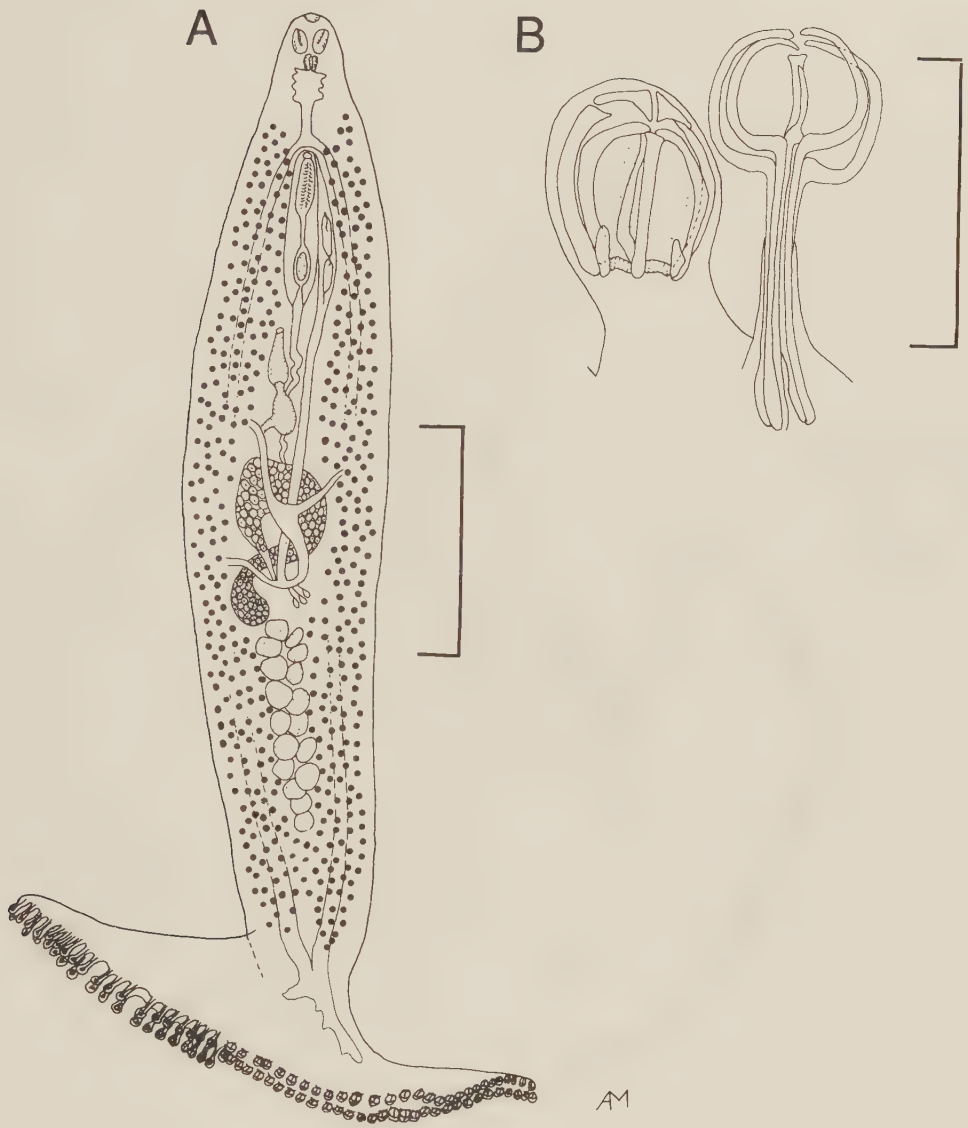


Figure 70

Pyragraphorus pyragraphorus: (**A**) ventral view. Scale: 1 mm; (**B**) clamps. Scale: 0.1 mm. Drawn from USNM 36559.

65(64) Haptor with approximately 37 clamps with accessory sclerites and multiple ribs (gastrocotylid type), hamuli at terminus of haptor; genital atrium armed with a circle of 12 spines. Parasitic on Spanish mackerels, *Scomberomorus maculatus*. . . . . ***Pseudaxine mexicana* (Fig. 71)**

65(64) Clamps lacking accessory sclerites and ribs (microcotylid type), hamuli at midpoint in clamp row; genital atrium armed or unarmed. . . . . **(Family Axinidae) 66**

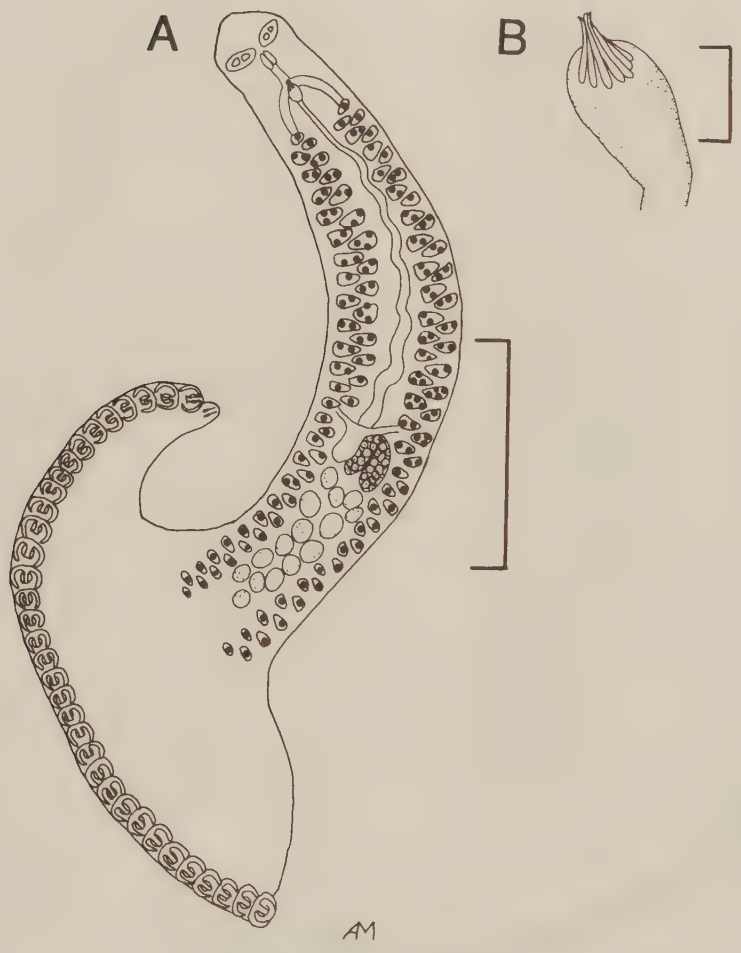


Figure 71
Pseudaxine mexicana: (**A**) ventral view. Scale: 0.5 mm; (**B**) genital atrium. Scale: 0.025 mm. Drawn from USNM 9167.

66(65) Haptor with approximately 46 clamps; genital atrium armed with 2 rows of lateral and 1 row of medial spines; male copulatory organ armed with circle of 12 spines; ovary U-shaped. Parasitic on silverstripe halfbeaks, *Hyporhamphus unifasciatus*. . . . . ***Axine hyporhampi* (Fig. 72)**

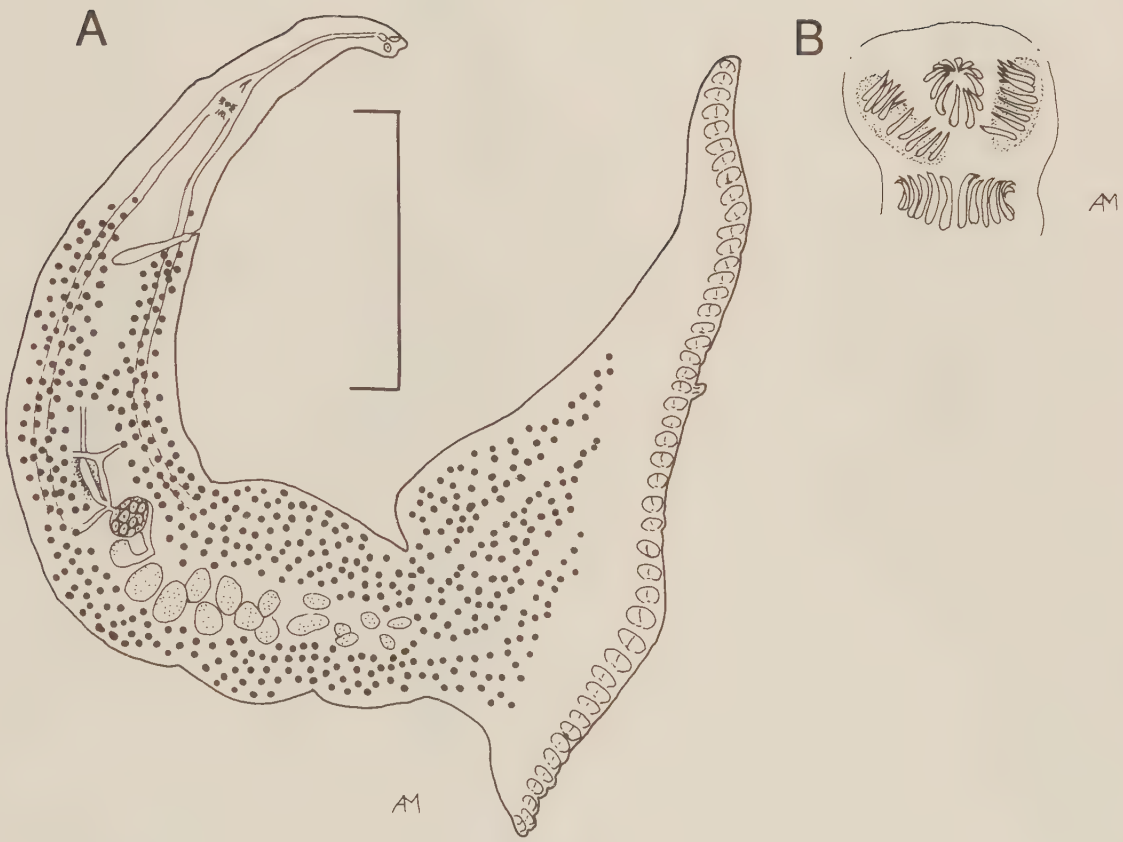


Figure 72

Axine hyporhampi: (**A**) ventral view. Scale: 0.5 mm; (**B**) genital atrium and cirrus spines. Drawn from USNM 36550.

66(65) Haptor with 42 to 82 clamps; genital atrium and male copulatory organ unarmed; ovary J-shaped. Parasitic on Atlantic needlefish..... ***Nudaciraxine gracilis*** **(Fig. 73)**

67(63) Clamps with accessory sclerites and multiple ribs (gastrocotylid type)..... **68**

67(63) Clamps lack accessory sclerites and multiple ribs (microcotylid type)..... **71**

68(67) Clamps confined to haptor proper..... **69**

68(67) Clamps along lateral body margins..... **70**

69(68) Haptor with about 80 somewhat asymmetric clamps in two equal rows; vitellaria not extending into haptor; male copulatory organ with numerous short spines. Parasitic on bluefish, *Pomatomus saltatrix*, striped bass, *Morone saxatilis*, and mackerels, *Scomberomorus* spp. ..... ***Gotocotyla acanthophallus*** **(Fig. 74)**

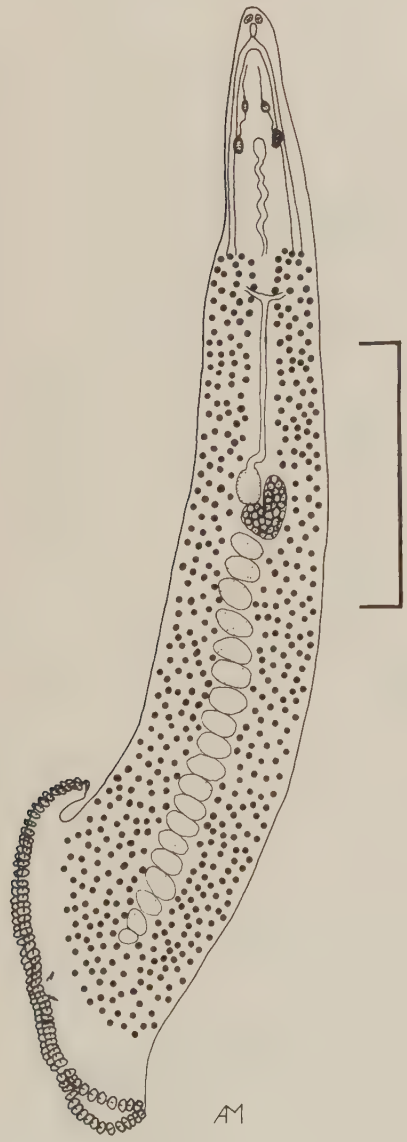


Figure 73
Nudaciraxine gracilis: ventral view. Scale: 1 mm. Drawn from USNM 37723.

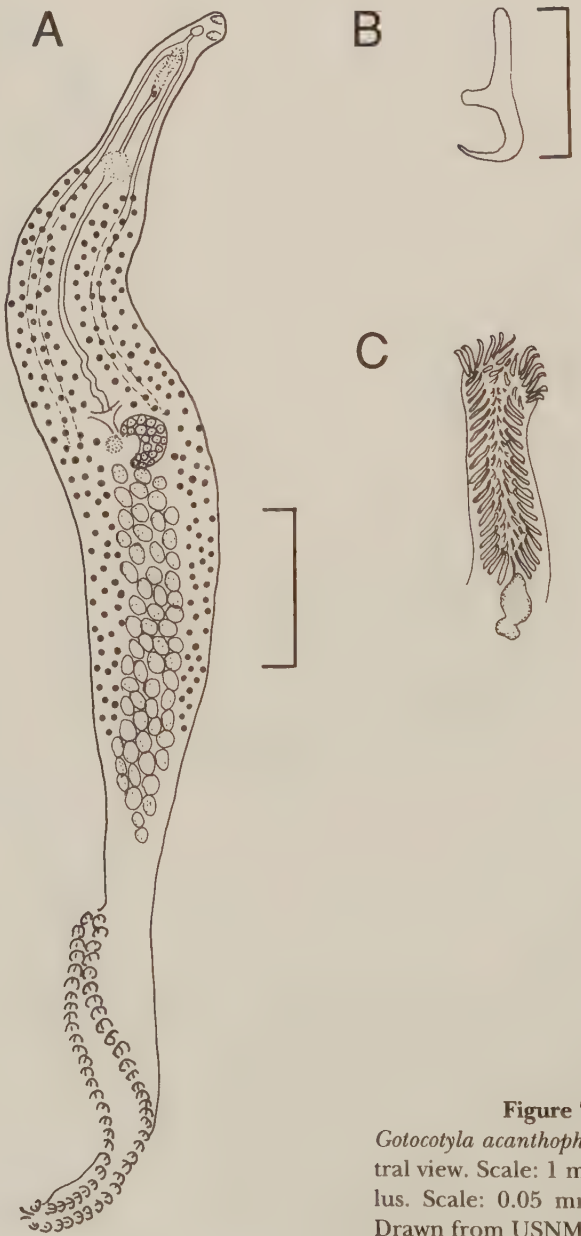


Figure 74
Gotocotyla acanthophallus: (**A**) ventral view. Scale: 1 mm; (**B**) hamulus. Scale: 0.05 mm; (**C**) cirrus. Drawn from USNM 36558.

69(68) Haptor with about 135 clamps in two unequal rows, a short row of 50 and a long row of 85 opposite; vitellaria extending into haptor; male copulatory organ with numerous elongate spines. Parasitic on mackerels. ..... *Scomberocotyle scomberomori* **(Fig. 75)**

Figure 75

Scomberocotyle scomberomori: (**A**) ventral view. Scale: 1 mm; (**B**) cirrus and genital atrium. Scale: 0.1 mm. Drawn from USNM 37494.

70(68) Haptor footlike with about 40 clamps; testes few, large; vitellaria confined to ventral half of haptoral region. Parasitic on mackerels. ..... *Thoracocotyle crocea* **(Fig. 76)**

Figure 76

Thoracocotyle crocea: (**A**) ventral view. Scale: 1 mm; (**B**) clamp. Scale: 0.05 mm. Drawn from USNM 35588.

70(68) Haptor not footlike, with about 200 clamps in roughly equal rows; testes numerous, small; vitellaria not so confined. Parasitic on wahoo, *Acanthocybium solandri*. . . . . ***Neothoracocotyle acanthocybii*** **(Fig. 77)**

71(67) Clamps in distinctly unequal rows. . . . . **(Family Heteraxinidae) 72**

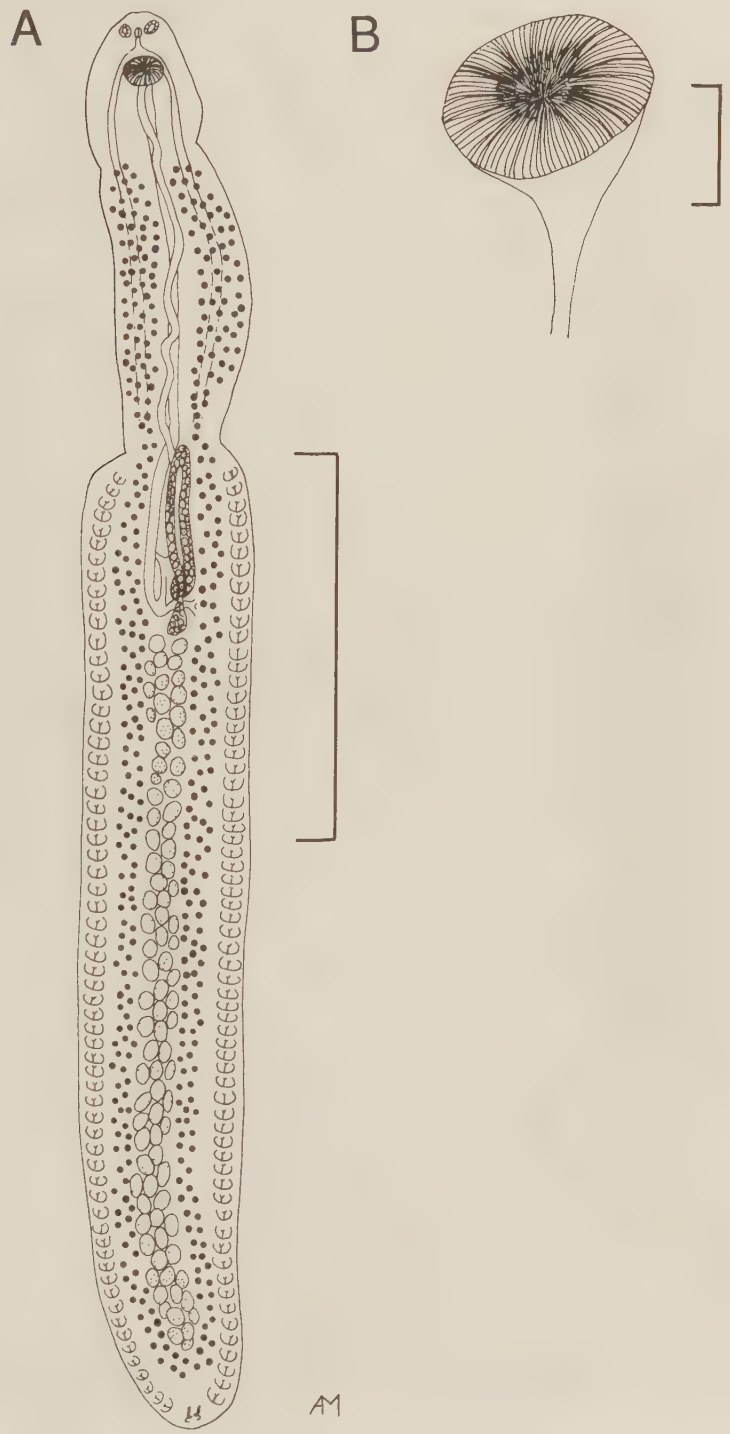


Figure 77
Neothoracocotyle acanthocybii: (**A**) ventral view. Scale: 2 mm; (**B**) genital atrium. Scale: 0.1 mm. Drawn from USNM 38132.

71(67) Clamps in approximately equal rows. ..... **(Family Microcotylidae) 73**

72(71) Clamps asymmetrical, unequal in size and shape, clamps in the long row larger, about 36–55 in number, clamps of the short row 11–17 in number; genital atrium and male copulatory organ armed with more than 30 spines. Parasitic on jacks, *Caranx* spp. ..... ***Cemocotyle* spp. (Fig. 78)**

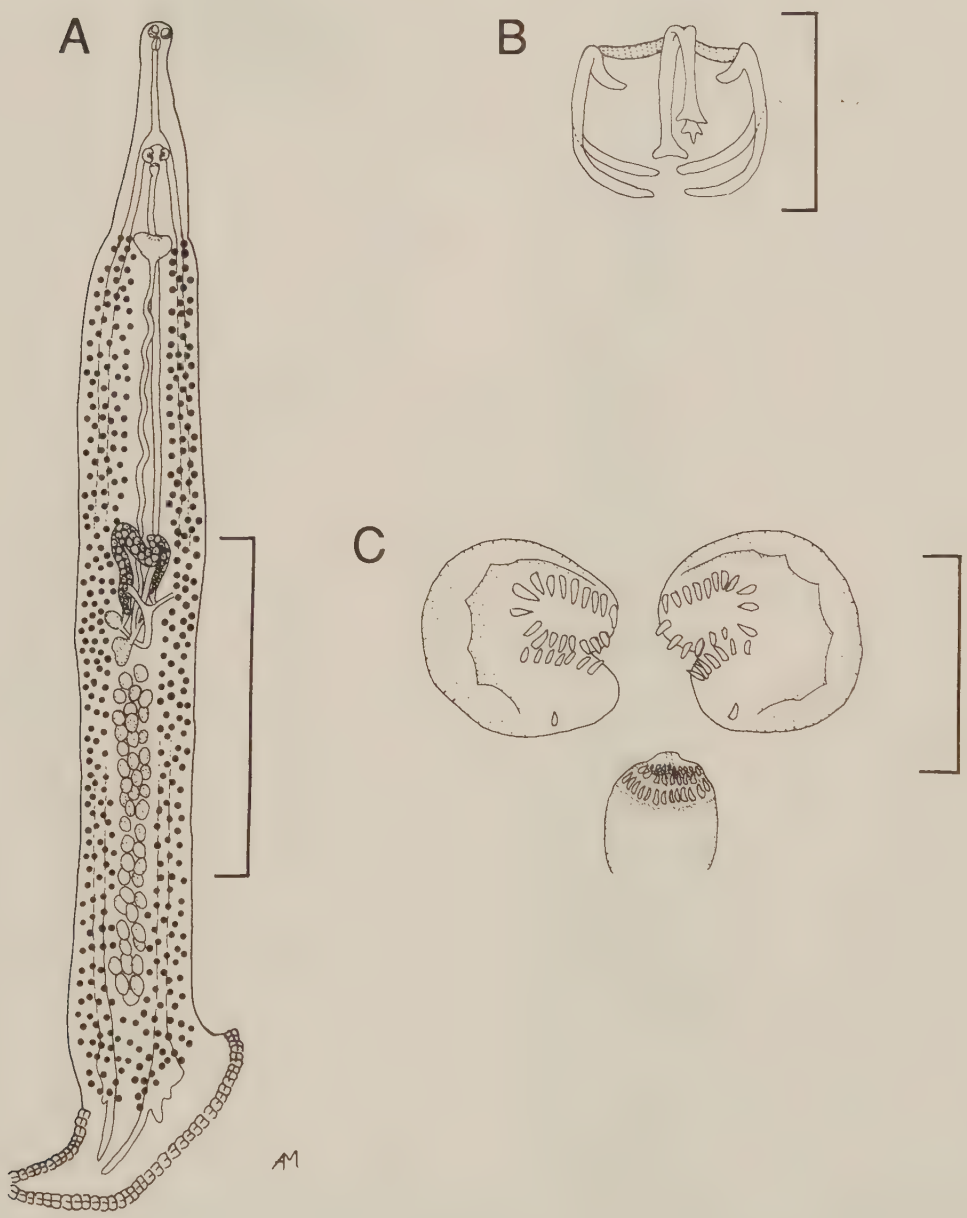


Figure 78
Cemocotyle noveboracensis: (**A**) ventral view. Scale: 2 mm; (**B**) clamp. Scale: 0.05 mm; (**C**) genital atrium and cirrus. Scale: 0.1 mm. Drawn from USNM 37738.

72(71) Clamps symmetric and approximately equal in size and shape, with 25–35 in the long row and 18–21 in the short row; genital atrium armed with fewer than 20 spines; male copulatory organ unarmed. Parasitic on spot, *Leiostomus xanthurus*. ..... ***Heteraxinoides xanthophilis*** **(Fig. 79)**

73(71) Genital atrium unarmed. **74**

73(71) Genital atrium armed with spines. **75**

Figure 79

Heteraxinoides xanthophilis: (**A**) ventral view. Scale: 0.5 mm; (**B**) clamp. Scale: 0.025 mm; (**C**) genital atrium spines. Scale: 0.05 mm. Drawn from USNM 38158.

74(73) Clamps in double rows on each side of haptor; male copulatory organ unarmed. Parasitic on black drum, *Pogonias cromis*. ..... ***Pauciconfibula pogoniae*** **(Fig. 80)**

74(73) Clamps in a single row on each side of haptor; male copulatory organ armed with spines. Parasitic on striped bass. ..... ***Gamacallum macroura*** **(Fig. 81)**

Figure 80
Pauciconfibula pogoniae: ventral view. Scale: 2 mm. Drawn from USNM 35090.

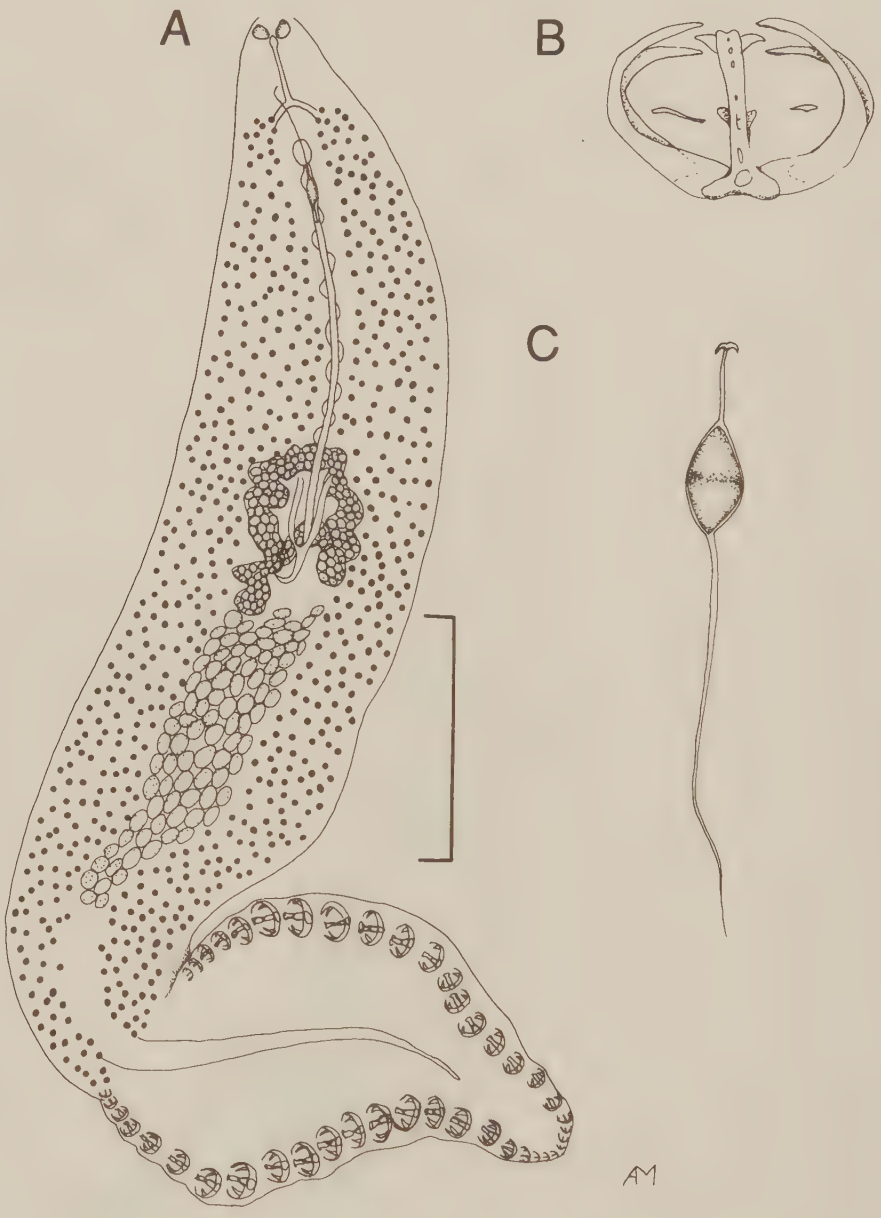


Figure 81
Gamacallum macroura: (**A**) ventral view. Scale: 2 mm; (**B**) clamp; (**C**) egg. Drawn from USNM 36525.

75(74) Genital atrium with 6 to 7 lateral muscular suckerlike pockets, armed with 3 rows of spines. Parasitic on seatrout, *Cynoscion* spp. ..... ***Cynoscionicola* spp. (Fig. 82)**

75(74) Genital atrium lacking lateral pockets. **76**

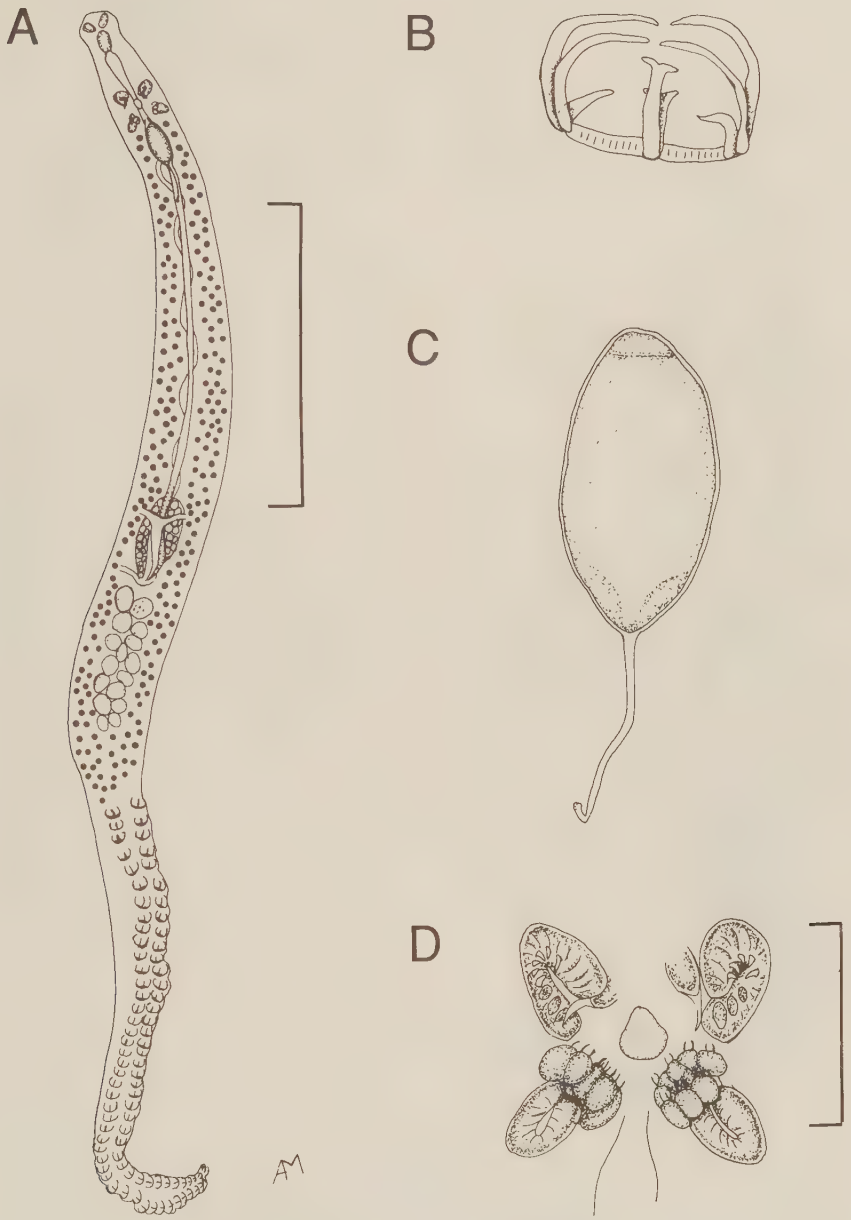


Figure 82
Cynoscionicola pseudoheteracantha: (**A**) ventral view. Scale: 1 mm; (**B**) clamp; (**C**) egg; (**D**) genital atrium complex. Scale: 0.1 mm. Drawn from USNM 38251.

76(75) Vitellaria extend to posterior end of body proper; genital atrium usually armed with a circle or patch of spines. Parasitic on perciform fishes. ..... ***Microcotyle* spp. (Fig. 83)**

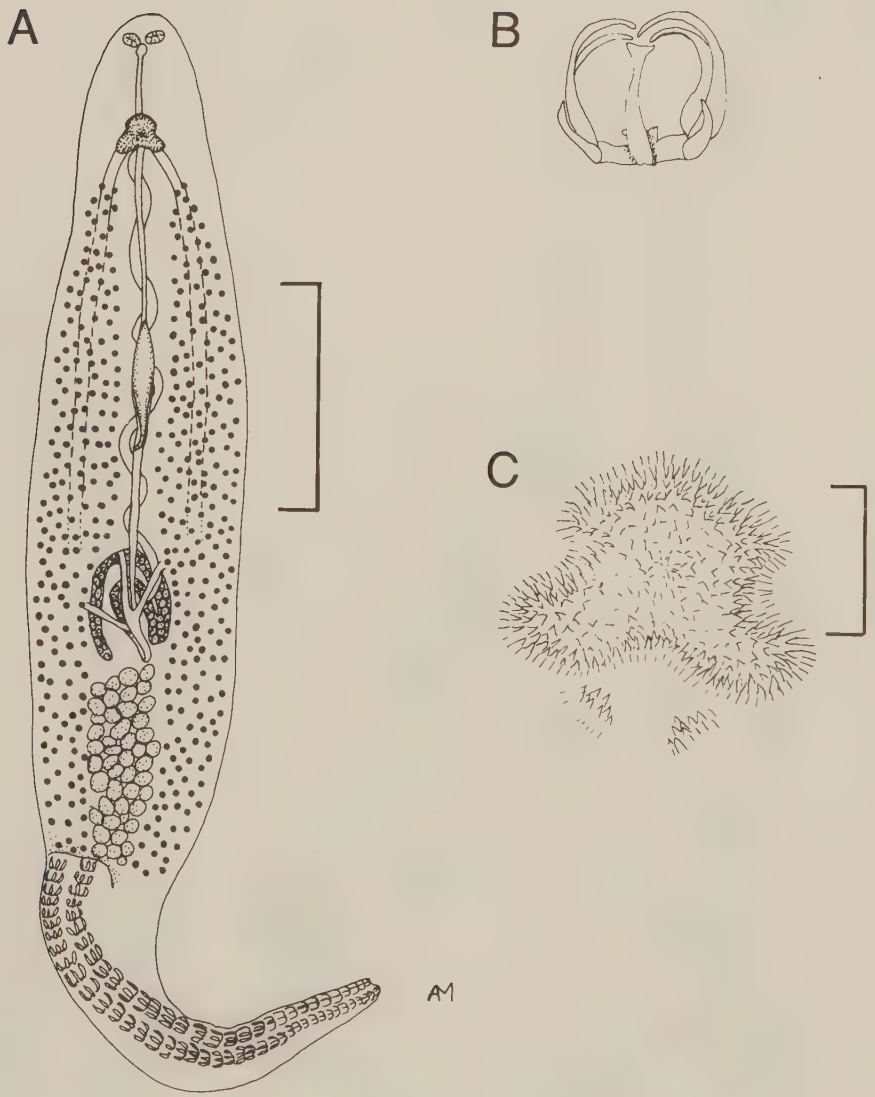


Figure 83

Microcotyle pomatomi: (**A**) ventral view. Scale: 0.5 mm; (**B**) clamp; (**C**) genital atrium spines. Scale: 0.05 mm. Drawn from specimens collected from bluefish, *Pomatomus saltatrix*, off Beaufort, North Carolina.

76(75) Vitellaria do not reach end of body; genital atrium armed with 15 to 20 pairs of spines in 3 groups. Parasitic on striped mullet..... *Metamicrocotyla macracantha* **(Fig. 84)**

Figure 84

Metamicrocotyla macracantha: (**A**) ventral view. Scale: 2 mm; (**B**) clamp; (**C**) genital atrium spines. Drawn from USNM 38253.

Annotated Systematic List

Numerous authors have contributed to reports of the monogeneans, as well as the one udonellid discussed below, from fish hosts of the estuarine and marine coastal waters from the U.S.-Canada border to Beaufort, North Carolina. All known records for this region are given for each of the 108 species. In addition, annotated references to their biology and morphology are included. No attempt is made here to give individual global records for those species with cosmopolitan distributions or to cite reports of their occurrence in distant geographic locations. The taxonomic system followed in this manual is generally a modification of the scheme of Llewellyn (1970) as used by Beverley-Burton (1984) for Canadian monogeneans. Superfamilies, families, genera, and species are arranged alphabetically within each of the orders of the class. Several general references that may prove useful in the study of Monogenea include Hargis (1957a), Koratha (1955a), Lebedev (1979), Margolis and Arthur (1979), Price (1939b), Rohde (1978b, 1979, 1981, and 1986), and Schell (1985). For older literature and synonyms, see Baer and Euzet (1961), Hargis et al. (1969, 1970, 1971, 1972, and 1982), Sproston (1946), or Yamaguti (1963). Scientific as well as common names of fishes are included when known and follow Special Publication No. 20 of the American Fisheries Society (Robins et al., 1991).

Class UDONELLIDEA Ivanov, 1952
Order UDONELLIDA Ivanov and Mamkaev, 1973

Family UDONELLIDAE Taschenberg, 1879

***Udonella caligorum* Johnston, 1835**

Synonyms: *Nitzschia papillosa* Linton, 1898; *Lintonia papillosa* (Linton, 1898) Monticelli, 1904; *Calinella myliobati* Guberlet, 1936; *Udonella socialis* Linton, 1910; and several others.

Records: Atlantic cod, *Gadus morhua*, Woods Hole (Linton, 1898), Georges Bank (Linton, 1940); lumpfish, *Cyclopterus lumpus*, and little tunny, *Euthynnus alletteratus*, off Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: *Udonella caligorum* is found as a hyperparasite on copepods, such as *Caligus* spp., themselves parasitic on the gills of a variety of fish hosts. For example, this species has been reported from the parasitic copepod *Caligus praetextus* in the mouth and skin of red drums, *Sciaenops ocellatus*, in Mississippi Sound and at Palacois, Texas (Overstreet, 1983a and 1983b), and on the isopod *Livoneca vulgaris* off San Francisco, California (Crane, 1972). *Udonella caligorum* is distributed along both the Atlantic and Pacific coasts of North and South America as well as off the coasts of Europe, Australia, and New Zealand. Halton and Jennings (1965) provided some information on its feeding and digestive processes; Kabata (1973) and Villalba (1985) gave the distribution and probable feeding habits on copepod hosts in Scottish and Chilean waters, respectively. Schell (1972) described early development. Justine et al. (1985) briefly described sperm ultrastructure; Rohde et al. (1989) examined the fine structure of sperm, sense receptors, flame bulbs, and tegument as a basis for phylogenetic position. Price (1938b) and Nichols (1975) described the morphology and possible taxonomic relationships. *Udonella caligorum* is included in this manual because of its cooccurrence with monogeneans on fish gills.

Class MONOGENEA Carus, 1863
Order MICROBOTHRIIDEA Lebedev, 1988

The microbothriids as well as the "monocotylids" (families Monocotylidae and Loimoidae) are assigned to orders following the scheme of Lebedev (1988) and Boeger and Kritsky (1993). Earlier, Llewellyn (1970) and Beverley-Burton (1984) mentioned the uncertain relationships of the families with other monogeneans. Lawler (1981) gave an extensive review of the zoogeography and host specificity of members of the superfamily Capsaloidea using Price's (1936) scheme, which includes the present orders Microbothriidea, Monocotylidea, and portions of Dactylogyrida.

Family MICROBOTHRIIDAE Price, 1936

***Dermophthirius carcharhini* MacCallum, 1926a**

Synonyms: None.

Records: On the skin and nasal cavities of what is probably the dusky shark, *Carcharhinus obscurus* (reported by MacCallum [1926a] as *Carcharhinus commersonii*), Woods Hole, Massachusetts. The exact species represented by this host name is questionable (Lawler, 1981).

Remarks: Also reported from the skin of the blacktip shark, *Carcharhinus limbatus*, off Grand Isle, Louisiana, and Mississippi (Thatcher, 1959). Benz (1987) suggested that the specimens identified by Thatcher (1959) may be *D. penneri*. Cheung and Ruggieri (1983) believed that specimens reported as *D. carcharhini* from sharks off Senegal by Euzet and Maillard (1967) may be *D. nigrellii*. It was redescribed by Price (1938b), but Cheung and Ruggieri (1983) pointed out a misinterpretation of the haptor structure by Price. Rand et al. (1986) described its attachment to the Galapagos shark, *C. galapagensis*.

***Dermophthirius penneri* Benz, 1987**

Synonyms: None.

Records: On the body surface of the blacktip shark, New Jersey (Benz, 1987).

Remarks: Benz (1987) also reported it from the Gulf of Mexico, off Florida.

***Microbothrium apiculatum* Olsson, 1869**

Synonyms: *Dermophagus squali* MacCallum, 1926b, and *Philura orata* MacCallum, 1926a.

Records: On the skin in the cloacal region of the spiny dogfish, *Squalus acanthias*, Chesapeake Bay (Zwerner and Lawler, 1972), and Woods Hole, Massachusetts (MacCallum, 1926, a and b); probably the dusky shark, *Carcharhinus obscurus* (reported as *Carcharhinus commersonii*), Woods Hole (MacCallum, 1926, a and b).

Remarks: Other geographic records include Canada (Beverley-Burton, 1984) and the eastern Atlantic. Price (1938b) redescribed the species and (1963) reviewed the family and gave a key to the species of *Microbothrium*.

***Neodermophthirius harkemai* Price, 1963**

Synonyms: *Cadenatia polytestis* Euzet and Maillard, 1967.

Record: On the gills of the lemon shark, *Negaprion brevirostris*, North Carolina (Price, 1963).

Remarks: Also reported off Senegal by Euzet and Maillard (1967).

Order MONOCOTYLIDEA Lebedev, 1988
Family LOIMOIDAE Bychowsky, 1957

***Loimopapillosum dasyatis* Hargis, 1955e**

Synonyms: None.

Record: On the gills of the bluntnose stingray, *Dasyatis say*, Chesapeake Bay (McMahon, 1963).

Remarks: Also reported from stingrays collected at Alligator Harbor, Florida (Hargis, 1955e).

***Loimos salpinggoides* MacCallum, 1917**

Synonyms: None.

Records: On the gills of the dusky shark, Woods Hole (MacCallum, 1917).

Remarks: Price (1938b) redescribed the species, and Manter (1944) supplemented its description.

***Loimos scoliodoni* (Manter, 1938) Manter, 1944**

Synonyms: *Tricotyle scoliodoni* Manter, 1938.

Records: On the gills of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, Beaufort, North Carolina (Manter, 1938).

Remarks: Also found on sharks from Alligator Harbor, Florida (Hargis, 1955e), and Texas by Koratha (1955b), who also redescribed it.

Family MONOCOTYLIDAE Taschenberg, 1879

***Cathariotrema selachii* (MacCallum, 1916b) Johnston and Tiegs, 1922**

Synonyms: *Monocotyle selachii* MacCallum, 1916b, and *Paramonocotyle selachii* (MacCallum, 1916b) Johnston, 1934.

Records: In the nasal cavities of the thresher shark, *Alopias vulpinus*; dusky shark; and the smooth hammerhead, *Sphyrna zygaena* (MacCallum, 1916b); "shark" (reported as *Carcharias commersonii* by Price, 1938b), all at Woods Hole, Massachusetts.

Remarks: Redescribed by Price (1938b).

***Dasybatotrema dasybatis* (MacCallum, 1916b) Price, 1938b**

Synonyms: *Monocotyle dasybatis* MacCallum, 1916b, and *Monocotyloides dasybatis* (MacCallum, 1916b) Johnston, 1934.

Records: On the gills of the roughtail stingray, *Dasyatis centroura*, Woods Hole, Massachusetts (MacCallum, 1916b).

Remarks: Price (1938b) redescribed the species. Euzet and Maillard (1967) gave a detailed description of the haptor and revised the generic diagnosis based on specimens from *Dasyatis marmorata* taken off Senegal, Africa. Young (1967) revised the generic diagnosis.

***Empruthotrema raiae* (MacCallum, 1916b) Johnston and Tiegs, 1922**

Synonyms: *Acanthocotyle raiae* MacCallum, 1916b.

Records: In the nasal fossae of the little skate, *Raja erinacea*, and winter skate, *R. ocellata*, Woods Hole, Massachusetts (MacCallum, 1916b); gills of the clearnose skate, *R. eglanteria*, Chesapeake Bay (McMahon, 1963).

Remarks: Also reported from Alligator Harbor, Florida (Hargis, 1955e). Redescribed by Price (1938b) and Kearn (1976), who also described the oncomiracidium and gave an emended generic diagnosis based on specimens from eastern Atlantic rajids. Whittington and Kearn (1992) also emended the generic diagnosis.

***Heterocotyle minima* (MacCallum, 1916b) Price, 1938b**

Synonyms: *Monocotyle dasybatis minimus* MacCallum, 1916b; *Trionchus dasybatis* MacCallum, 1916b; *Monocotyle minima* (MacCallum, 1916b) Johnston and Tiegs, 1922; and *Monocotyloides minimus* (MacCallum, 1916b) Johnston, 1934. *Heterocotyle minimus* may be a synonym of *H. (Monocotyle) pastinacae* Scott, 1904, a species insufficiently described at this time.

Records: On the gills of the roughtail stingray and spiny dogfish, Woods Hole, Massachusetts (MacCallum, 1916b).

Remarks: Redescribed by Price (1938b). Young (1967) reviewed the genus and produced a key to species.

***Monocotyle diademalis* Hargis, 1955d**

Synonyms: *Heterocotyloides diademalis* (Hargis, 1955d) Yamaguti, 1963.

Records: On the gills of the bluntnose stingray and southern stingray, *Dasyatis americana*, Chesapeake Bay (McMahon, 1963).

Remarks: Also known from dasyatids collected at Alligator Harbor, Florida (Hargis, 1955d). Timofeeva (1984) emended the generic diagnosis and produced a key to the species of *Monocotyle*. Measures et al. (1990) emended the subfamily and generic diagnoses and provided a phylogenetic analysis of the genus.

***Monocotyle pricei* Pearse, 1949**

Synonyms: *Heterocotyloides pricei* (Pearse, 1949) Yamaguti, 1963.

Records: On the gills of southern and bluntnose stingrays, Chesapeake Bay (McMahon, 1963). Also reported from the gills of sheepshead, *Archosargus probatocephalus*, collected at Beaufort, North Carolina (Pearse, 1949). Hargis (1955d) considered this an accidental or abnormal host.

Remarks: Redescribed by Hargis (1955d) from Alligator Harbor, Florida, material. Kingston et al. (1969) described the oncomiracidium.

***Papillicotyle floridana* (Pratt, 1910) Young, 1967**

Synonyms: *Monocotyle floridana* Pratt, 1910; *Heterocotyle floridana* (Pratt, 1910) Price, 1938b; *Heterocotyle aetobatis* Hargis, 1955d; and *Alloheterocotyla aetobatis* Yamaguti, 1968.

Records: On the gills of the spotted eagle ray, *Aetobatis narinari*, Beaufort, North Carolina (Pearse, 1949).

Remarks: Reported from the Tortugas, Florida (Pratt, 1910), the Gulf coast of Florida (Hargis, 1955d), and Hawaii (Yamaguti, 1968). Redescribed by Price (1938b). In addition, Young (1967) noted that this species has 10, not 8, radial septa.

***Thaumatocotyle dasybatis* (MacCallum, 1916b) Price, 1938b**

Synonyms: *Merizocotyle dasybatis* MacCallum, 1916b, and *Pseudomerizocotyle dasybatis* (MacCallum, 1916b) Kay, 1942.

Records: In the nasal fossae (MacCallum, 1916b) and on the gills of the roughtail stingray and the little skate, Woods Hole, Massachusetts (Price, 1938b).

Remarks: Redescribed by Price (1938b). This may be a synonym of *T. concinna* Scott, 1904 (see Brinkmann, 1940; Lawler, 1981).

Order DACTYLOGYRIDA Bychowsky, 1937

Family ACANTHOCOTYLIDAE Price, 1936

***Pseudacanthocotyla verrilli* (Goto, 1899) Yamaguti, 1963**

Synonyms: *Acanthocotyle verrilli* Goto, 1899, and *A. borealis* Brinkmann, 1940.

Records: On the skin of the little skate, Maine (Manter, 1925 and 1926), and Cape Cod, Massachusetts (Goto, 1899); and the thorny skate, *R. radiata*, Cape Cod (Goto, 1899).

Remarks: Also reported from Canada, Greenland, Iceland, Norway, and the Bering Sea. Redescribed by Price (1938b). Using histochemical techniques, Joffe and Kotikova (1988) demonstrated cholinesterase in the nervous system.

Family AMPHIBDELLIDAE Bychowsky, 1957

***Amphibdella flavolineata* MacCallum, 1916b**

Synonyms: None.

Records: On the primary gill mucosa of the Atlantic torpedo, *Torpedo nobiliana*, Woods Hole, Massachusetts (MacCallum, 1916b), and Menemsha Bight near Woods Hole (Linton, 1940); "stingray," Woods Hole (Price, 1937).

Remarks: Redescribed by Price (1937). This species was also reported from the Irish Sea, off southern England, and the Mediterranean. A detailed account of its biology, morphology, and taxonomy was given by Llewellyn (1960). Juveniles are found in the heart ventricle of the host, and Lyons (1971) described epidermal ultrastructure of these juveniles as well as the gill-dwelling adults.

***Amphibdelloides maccallumi* (Johnston and Tiegs, 1922) Price, 1937**

Synonyms: *Amphibdelloides torpedinis* Parona and Perugia, 1890b, not Chatin, 1874; *A. torpedinis* MacCallum, 1916b; and *Amphibdella maccallumi* Johnston and Tiegs, 1922.

Records: On the secondary gill lamellae of the spiny dogfish, Woods Hole, Massachusetts (Price, 1937); and Atlantic torpedo, Woods Hole (MacCallum, 1916b; Price, 1937).

Remarks: Records of the species beyond the range of this manual include the Irish Sea, Irish Atlantic Slope, off Plymouth, England, Mediterranean Sea, off California, and New Zealand. Redescribed by Alexander (1954), Llewellyn (1960), and Dillon and Hargis (1965a). Llewellyn (1960) studied its morphology and biology and provided a list of amphibdellids from electric rays (Torpedinidae). According to Llewellyn (1960), the oncomiracidium described by Euzet (1957) was believed to be that of either this species or *A. vallei*. Lyons (1966) provided histochemical data on hamuli and marginal hooks.

Family ANCYROCEPHALIDAE Bychowsky and Nagibina, 1978

***Ancyrocephalus parvus* Linton, 1940**

Synonyms: None.

Records: On the gills of the Atlantic needlefish, *Strongylura marina*, Woods Hole, Massachusetts (Linton, 1940), and Chesapeake Bay (Kingston et al., 1969).

Remarks: Also reported from Alligator Harbor, Florida (Hargis, 1955b), off Alabama by Williams and Rogers (1972), and on redfin needlefish, *S. notata*, in Biscayne Bay, Florida (Skinner, 1978). The species was redescribed by Williams and Rogers (1972), and Kingston et al. (1969) described the oncomiracidium.

Family BOTHITREMATIDAE Bychowsky, 1957

***Bothitrema bothi* (MacCallum, 1913c) Price, 1936**

Synonyms: *Acanthocotyle bothi* MacCallum, 1913c.

Records: On the gills of the windowpane, *Scophthalmus aquosus*, Woods Hole, Massachusetts (MacCallum, 1913c, 1916a, and 1917), and New Jersey (Meyers, 1978). Also occasionally found in nares of New Jersey windowpanes (this publication).

Remarks: Price (1937) redescribed this species.

Family CAPSALIDAE Baird, 1853

Lawler (1981) gave an extensive review of the zoogeography and host specificity of members of the superfamily Capsaloidea using the scheme of Price (1936). Stunkard (1962) as well as Wheeler and Beverley-Burton (1987) pointed out the problems in clearly delineating genera within the subfamily Capsalinae.

***Benedeniella posterocolpa* (Hargis, 1955e) Yamaguti, 1963**

Synonyms: *Benedenia posterocolpa* Hargis, 1955e.

Records: On the ventral surface skin of the cownose ray, *Rhinoptera bonasus*, Chesapeake Bay (McMahon, 1963).

Remarks: Also reported from this host in Tampa Bay, Florida (Hargis, 1955e).

***Caballerocotyla manteri* (Price, 1951) Price, 1960**

Synonyms: *Capsala manteri* Price, 1951.

Records: On the gills of the little tunny, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Price (1951) reported this species off the Tortugas, Florida. Mamaev (1968) described the subspecies, *C. m. affinis* from South China Sea scombrids. Price (1960), Stunkard (1962), Wagner and Carter (1967), and Bussieras (1972) gave keys to the species. Justine et al. (1985) described spermatozoan ultrastructure; and Justine and Mattei (1987) described spermatogenesis. Yamaguti (1968) considered *Caballerocotyla* to be a subgenus of *Capsala*.

***Capsala martinierei* Bosc, 1811**

Synonyms: None.

Records: On the skin of ocean sunfish, *Mola mola*, Atlantic coast from Newfoundland (Threlfall, 1967) and Nova Scotia, Canada (Logan and Odense, 1974).

Remarks: This species has also been reported from the eastern Atlantic Ocean, Mediterranean Sea, and the Pacific coast of North America and Chile. Price (1939a) redescribed the adult. Logan and Odense (1974) studied the skin pathology caused by this worm, and Kearn (1963) described the oncomiracidium. There is a great deal of confusion in the literature over the identification of this species as well as its separation from *Tricotyla molae* and *Tristoma coccineum*. This species has not yet been reported from this manual's range, but it is included because of the cosmopolitan distribution of its host and the proximity of the Canadian records.

***Capsaloides cornutus* (Verrill, 1875) Price, 1939a**

Synonyms: *Tristoma cornutum* Verrill, 1875; *Capsala cornuta* (Verrill, 1875) Johnston, 1929; and *Capsaloides cornutum* (Verrill, 1875) Price, 1938a.

Records: On the gills of white marlin, *Tetrapturus albidus*, Woods Hole, Massachusetts, and the Block Island region, Rhode Island (Verrill, 1875; Price, 1939a).

Remarks: Price (1960) gave a key to the species.

***Capsaloides magnaspinosus* Price, 1939a**

Synonyms: None.

Records: In the nares of white marlin, Woods Hole, Massachusetts (Price, 1939a).

Remarks: The description is based on three specimens collected by MacCallum.

***Entobdella bumpusii* (Linton, 1900) Johnston, 1929**

Synonyms: *Epibdella bumpusii* Linton, 1900; *Epibdella (Phylline) bumpusii* (Linton, 1900) Monticelli, 1902; *Phylline bumpusii* (Linton, 1900) Linstow, 1903; *Phyllonella bumpusii* (Linton, 1900) MacCallum, 1927; and *Entobdella (Parepibdella) bumpusii* (Linton, 1900) Johnston, 1929.

Records: On the skin and gills of the roughtail stingray, Woods Hole, Massachusetts (Linton, 1900).

Remarks: Redescribed by Price (1939a). Linton (1908) described the genitalia and egg formation. Crane (1972) gave a key to the species. Lyons (1966) reported histochemical tests on hamuli and marginal hooks. Klassen et al. (1989) reviewed and revised the genus, giving an emended diagnosis and key to species.

***Entobdella hippoglossi* (Müller, 1776) Blainville, 1818**

Synonyms: *Phylonella hippoglossi* (Müller, 1776) Goto, 1899; *Epibdella (Phylline) hippoglossi* (Müller, 1776) Monticelli, 1902; *Entobdella (Entobdella) hippoglossi* (Müller, 1776) Johnston, 1929; *Epibdella bumpusii* of Canavan, 1934; *Entobdella brattstroemi* Brinkmann, 1952; *E. curvunca* Ronald, 1957; *E. rosaceus* Crane, 1972; *E. steingroeveri* (Cohn, 1916) Johnston, 1929; *E. squamula* (Heath, 1902) Johnston, 1929.

Records: On the skin of Atlantic halibut, *Hippoglossus hippoglossus*, from Woods Hole, Massachusetts, and Swans Island, Maine (Price, 1939a).

Remarks: Also reported from this host off Nova Scotia, Greenland, Iceland, northern Europe, Alaska, the Bering Sea, and the Barents Sea; arrowtooth flounder, *Atheresthes stomias*, Bering Sea; Pacific halibut, *H. stenolepis*, eastern Pacific and Bering Sea. Reported by Meserve (1938) on the bullseye puffer, *Sphoeroides annulatus*. This record is considered erroneous by modern workers (Lawler, 1981). Halton and Jennings (1965) reported some aspects of nutrition, and Arme (1977) reported on the amino acid composition. Kearn (1974a) gave information on larval hatching and (1974b) described the oncomiracidium. Klassen et al. (1989) provided comparative morphometric data.

***Nasicola klawei* (Stunkard, 1962) Yamaguti, 1968**

Synonyms: *Tristoma* sp. of Rossignol and Repelin, 1962, and *Caballerocotyla klawei* Stunkard, 1962.

Records: In the nasal capsules of yellowfin tuna, *Thunnus albacares*, off New York (Bane, 1969).

Remarks: Additional reports from *T. albacares* include Puerto Rico, Bahamas, Venezuela, Gulf of Guinea, eastern Atlantic Ocean, and the Pacific Ocean off northern Peru and Hawaii (reported as *Neothunnus macropterus* by Stunkard [1962]); blackfin tuna, *T. atlanticus*, Puerto Rico; and tuna, Hawaii. Bane (1969) gave comparative measurements of worms from the two Atlantic hosts.

***Nitzschia sturionis* (Abildgaard, 1794) Krøyer, 1852**

Synonyms: *Phylline sturionis* (Abildgaard, 1794) Monticelli, 1908.

Records: On the gills of the Atlantic sturgeon, *Acipenser oxyrhynchus*, New Brunswick, Canada (Appy and Dadswell, 1978).

Remarks: This species is included because the record is near the geographic range of this manual. Also, *N. superba* may be a synonym of *N. sturionis* (Bychowsky, 1957). It has been reported from the gills of sturgeons from northern and eastern Europe. Timofeeva (1983) studied the nervous system. Gusev and Timofeeva (1986) described ciliary cells and chaetotaxy of the oncomiracidium, and Joffee et al. (1987) gave a description of the adult pharynx.

***Nitzschia superba* MacCallum, 1921**

Synonyms: *Nitzschia elegans* of Verrill (1875) and of Linton (1898) and *N. elongata* of Linton (1901).

Records: On the gills and inner surface of the operculum of shortnose sturgeon, *Acipenser brevirostrum*, Woods Hole, Massachusetts; and Atlantic sturgeon, Woods Hole (Linton, 1898).

Remarks: Redescribed by Price (1939a). Bychowsky (1957) considered this to be a synonym of *N. sturionis*. However, more work is needed to clarify the validity of this species.

***Tricotyla molae* (Blanchard, 1847) Guiart, 1938**

Synonyms: *Capsala molae* (Blanchard, 1847) Johnston, 1929; *Tricotyla cutanea* var. *mediterranea* or *T. c. microcotyla* of Guiart (1938); and *Tristomum rudolphianum* of Diesing (1850) and of Linton (1898 and 1900).

Records: On the skin of the ocean sunfish, Woods Hole, Massachusetts (Linton, 1898 and 1940), New Jersey (Leidy, 1890; Price, 1962c), and off Delaware (this publication).

Remarks: Also reported from the eastern Atlantic Ocean and Mediterranean Sea. Because of their similarity, past workers have probably confused *Tricotyla molae* with *Capsala martinierei*.

***Tristoma coccineum* Cuvier, 1817**

Synonyms: None.

Records: On the gills of smooth hammerhead, Woods Hole, Massachusetts; and swordfish, *Xiphias gladius*, Woods Hole (Price, 1939a) and northwest Atlantic (Iles, 1971).

Remarks: Iles (1971) detailed differences between *T. coccineum* and *T. integrum* from swordfish captured offshore along the middle Atlantic coast. This species is also known from the eastern Atlantic Ocean and Mediterranean Sea.

***Tristoma integrum* Diesing, 1850**

Synonyms: *Tristomum rotundum* Goto, 1894, and *T. coccineum* Cuvier, of Linton (1898, 1900, 1901, and 1940).

Records: On the gills of swordfish from the northwest Atlantic Ocean (Iles, 1971) and Woods Hole, Massachusetts (Price, 1939a).

Remarks: None.

***Tristomella laevis* (Verrill, 1875) Guiart, 1938**

Synonyms: *Tristoma laeve* Verrill, 1875; *Tristomum histiophori* Bell, 1891; *Tristomum laeve* var. *armata* Goto, 1899; and *Tristomella laeve* (Verrill, 1875) Johnston, 1929.

Records: In the mouth of white marlin, Block Island, Rhode Island (Verrill, 1875); gills of swordfish, Woods Hole and Block Island region (Linton, 1940).

Remarks: Also reported off Puerto Rico by Dyer et al. (1992), from the eastern and southern Atlantic Ocean (Pritchard, 1961), and off India on billfishes (Istiophoridae and Xiphiidae). Price (1938a) redescribed the species from Brazilian dolphin, *Coryphaena hippurus*.

***Tristomella lintoni* (Price, 1939a) Price, 1960**

Synonyms: *Tristoma laeve* of Linton (1898 and 1901) and *Capsala lintoni* Price, 1939a.

Records: On the gills of skipjack tuna, *Katsuwonus*

pelamis, near Martha's Vineyard, Massachusetts (Price, 1939a).

Remarks: The species description is based upon a single immature specimen.

***Tristomella onchidiocotyle* (Setti, 1899) Guiart, 1938**

Synonyms: *Tristomum onchidiocotyle* Setti, 1899; *Capsala onchidiocotyle* (Setti, 1898) Johnston, 1929; *Capsala onchidiocotyle* (Setti, 1899) Price, 1938a; and *C. maccallumi* Price, 1939a.

Records: On the gills of the little tunny, Woods Hole region (Price, 1939a).

Remarks: Also reported from tunas in the Mediterranean and off the coast of Angola.

Family DACTYLOGYRIDAE Bychowsky, 1933

***Haliotrema vanbenedeni* (Parona and Perugia, 1890a) Young, 1968**

Synonyms: *Tetronchus Van Benedenii* Parona and Perugia, 1890a; *Ancyrocephalus vanbenedenii* (Parona and Perugia, 1890a) Johnston and Tiegs, 1922; *Haplocleidus vanbenedeni* (Parona and Perugia, 1890a) Palombi, 1949; *Pseudohaliotrema mugilinus* Hargis, 1955c; and *Haliotrema mugilinus* (Hargis, 1955c) Yamaguti, 1963.

Records: On the gills of the striped mullet, *Mugil cephalus*, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported from mullets (Mugilidae) off Georgia (Rawson, 1976), Biscayne Bay (Skinner, 1975) and Alligator Harbor, Florida, Puerto Rico, and in the North, Mediterranean, and Black Seas. Gusev (1955) redescribed the species; Mizelle and Price (1964) gave a key to genera in the subfamily Ancyrocephalinae; and Young (1968) revised the genus. Garcia and Williams (1985) gave some temporal data on this species from Puerto Rico.

***Onchocleidus nactus* (Mayes and Johnson, 1975) Wheeler and Beverley-Burton, 1989**

Synonyms: *Urocleidus nactus* Mayes and Johnson, 1975, and *Pterocleidus nactus* (Mayes and Johnson, 1975) Beverley-Burton et al., 1986.

Records: On the gills of white perch, *Morone americana*, estuarine Abermarle Sound, North Carolina (Mayes and Johnson, 1975), and the lower Hudson River, New York (Liquori and Insler, 1985).

Remarks: Wheeler and Beverley-Burton (1989) supplemented the species description. Liquori and Insler (1985) gave data on seasonal fluctuations of *O. nactus* populations in the Hudson River.

***Protancyrocephaloides liopsettae* Burn, 1978**

Synonyms: None.

Records: On the gills of smooth flounder, *Pleuronectes putnami*, Great Bay, New Hampshire (Burn, 1978).

Remarks: Burn (1980) gave further information on the seasonal distribution of this species.

***Pseudohaliotrema longiphallus* (MacCallum, 1915) Young, 1967**

Synonyms: *Diplectanum longiphallus* MacCallum, 1915; *Ancyrocephalus longiphallus* (MacCallum, 1915) Johnston and Tiegs, 1922; *A. chaetodipteri* Pearse, 1949; and *Tetrancistrum longiphallus* (MacCallum, 1915) Price, 1937.

Records: On the gills of the Atlantic spadefish, *Chaetodipterus faber*, Chesapeake Bay (Zwerner and Lawler, 1972), and Beaufort, North Carolina (Pearse, 1949).

Remarks: Also reported from Biscayne Bay (Skinner, 1978) and Alligator Harbor, Florida.

Family DIONCIDAE Bychowsky, 1959

***Dionchus agassizi* Goto, 1899**

Synonyms: None.

Records: On the gills of the sharksucker, *Echeneis naucrates*, Chesapeake Bay (Zwerner and Lawler, 1972); spearfish remora, *Remora brachyptera*, Newport, Rhode Island (Goto, 1899); remora, *R. remora*, Woods Hole, Massachusetts (Linton, 1940).

Remarks: Also reported from echeneids in the Mediterranean Sea, and the Indian and Pacific Oceans. Redescribed by Price (1938b).

***Dionchus remorae* (MacCallum, 1916b) Price, 1938b**

Synonyms: *Acanthodiscus remorae* MacCallum, 1916b, and *Dionchotrema remorae* (MacCallum, 1916b) Johnston and Tiegs, 1922.

Records: On the gills of the sharksucker, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported from Alligator Harbor, Florida, the West Indies, eastern Mediterranean Sea, Great Barrier Reef, and the Madras coast of India. Justine and Mattei (1986) described ultrastructural observations on spermatozoa and (1987) some stages of fertilization. Timofeeva (1988) described genital structures in *Dionchus*, using *D. nagibinae*, and reported the presence of spermatophores. Whittington (1990) detailed the attachment of egg bundles to the gills of the remora.

Family DIPLECTANIDAE Bychowsky, 1957

***Diplectanum bilobatum* Hargis, 1955c**

Synonyms: None.

Records: On the gills of spotted seatrout, *Cynoscion nebulosus*, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported from Alligator Harbor, Florida, Mississippi, and Louisiana.

***Rhamnocercus bairdiella* Hargis, 1955c**

Synonyms: None.

Records: On the gills of silver perch, *Bairdiella chrysoura*, Chesapeake Bay (Kingston et al., 1969).

Remarks: Originally described from Alligator Harbor, Florida. Kingston et al. (1969) described the oncomiracidium.

***Rhamnocercus stichospinus* Seamster and Monaco, 1956**

Synonyms: None.

Records: On the gills of southern kingfish, *Menticirrhus americanus*, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported from gulf kingfish, *M. littoralis*, and Atlantic croaker, *Micropogonias undulatus*, from Texas (Seamster and Monaco, 1956).

Order GYRODACTYLIDA Bychowsky, 1937
Family GYRODACTYLIDAE Cobbold, 1864

Kritsky and Thatcher (1977) provided a key to the subfamilies and genera of these viviparous forms from North American hosts.

***Fundulotrema prolongis* (Hargis, 1955a) Kritsky and Thatcher, 1977**

Synonyms: *Gyrodactylus* sp. of Linton (1940) and *G. prolongis* Hargis, 1955a.

Records: On the skin of the sheepshead minnow, *Cyprinodon variegatus*, Chesapeake Bay (Zwerner and Lawler, 1972); skin of mummichog, *Fundulus heteroclitus*, Chesapeake Bay (Dillon, 1966), Bridgeport, Connecticut (Barkman and James, 1979), and Woods Hole (Linton, 1940); skin of striped killifish, *F. majalis*, Chesapeake Bay (Dillon, 1966).

Remarks: Also reported on various killifishes from the Gulf of Mexico to Canada. Redescribed by Williams and Rogers (1971). Cone and Odense (1988) emended the generic diagnosis and provided scanning electron microscope (SEM) micrographs.

***Gyrodactylus stephanus* Mueller, 1937**

Synonyms: None.

Records: On the skin of the sheepshead minnow, Chesapeake Bay (Zwerner and Lawler, 1972); skin of mummichog, Chesapeake Bay (Dillon, 1966), and Bridgeport, Connecticut (Barkman and James, 1979); skin of striped killifish, Chesapeake Bay (Dillon, 1966).

Remarks: Also reported from gulf killifish, *Fundulus grandis*, banded killifish, *F. diaphanus*, and ninespine stickleback, *Pungitius pungitius*. Mizelle and Kritsky (1967) produced a key to North American species of *Gyrodactylus*.

***Swingleus* sp. of Billeter (1974)**

Synonyms: None.

Records: On the skin of the mummichog, Freeport, New York (Billeter, 1974); striped killifish, Northport, New York (Billeter, 1974), and the Patuxent River of the Chesapeake Bay (Billeter[1]).

Remarks: Billeter (1974) had too few specimens for a species description, but he did state that the marginal hooks differed in size and shape from those of *S. polyclithroides* Rogers, 1969.

Order POLYOPISTHOCOTYLIDA (Odhner, 1912) emend. Beverley-Burton, 1984

Superfamily DICLYBOTHROIDEA Bychowsky, 1957
Family DICLYBOTHRIIDAE Bychowsky and Gusev, 1950

***Diclybothrium armatum* Leuckart, 1835**

Synonyms: None.

Records: On the gills of shortnose sturgeon, New Brunswick, Canada (Appy and Dadswell, 1978).

Remarks: This species is included because the record is near the geographic range of this manual. This species is also found on lake sturgeon, *Acipenser fulvescens*, in the Great Lakes and St. Lawrence River as well as on *Acipenser* spp. in Europe and Asia. Wright and Dechtiar (1974) showed some SEM features of surface structures. Gusev and Slusarev (1986) detailed oncomiracidial ciliary cells and chaetotaxy.

Superfamily HEXABOTHRIOIDEA Beverley-Burton, 1984
Family HEXABOTHRIIDAE Price, 1942

Euzet and Maillard (1974) reviewed the historical, systematic, and phylogenetic aspects of this family. Boeger and Kritsky (1989) discussed its phylogeny and coevolution with hosts and revised the family based on cladistic analysis.

***Erpocotyle maccallumi* (Price, 1942) Yamaguti, 1963**

Synonyms: *Squalonchocotyle canis* MacCallum, 1931, and *Neoerpocotyle maccallumi* Price, 1942.

Records: On the gills of the blacktip shark, Woods Hole, Massachusetts (MacCallum, 1931).

Remarks: Price (1942) redescribed the species. It has also been reported from *Paragaleus gruveli* (Carcharhinidae) off Senegal, Africa (Euzet and Maillard, 1967).

***Erpocotyle macrohystera* Price, 1942**

Synonyms: *Squalonchocotyle vulgaris* MacCallum, 1931, not Cerfontaine, 1899.

[1] Billeter, P., Department of Biology, Charles County Community College, LaPlata, MD 20646. Personal commun., August 1980.

Records: On the gills of the sandbar shark, *Carcharhinus plumbeus*, Woods Hole (MacCallum, 1931).

Remarks: Price (1942) redescribed the species.

***Erpocotyle mavori* (Linton, 1940) Yamaguti, 1963**

Synonyms: *Onchocotyle mavori* Linton, 1940, and *Neoerpocotyle mavori* (Linton, 1940) Price, 1942.

Records: Found on the bottom of an aquarium containing white perch at Woods Hole (Linton, 1940).

Remarks: Boeger and Kritsky (1989) considered this species incertae sedis, belonging to an as yet undefined genus. Because hexabothriids are parasites of elasmobranchs, the normal host is probably a shark (Boeger and Kritsky, 1989).

***Erpocotyle microstoma* (Brooks, 1934) Yamaguti, 1963**

Synonyms: *Neoerpocotyle microstoma* Price, 1942.

Records: On the gills of the smooth hammerhead, North Carolina (Brooks, 1934).

Remarks: Also reported from the great hammerhead, *Sphyrna mokarran*, in the Pacific Ocean near the Panama Canal and redescribed by Caballero et al. (1956) from this material.

***Erpocotyle sphyrnae* (MacCallum, 1931) Price, 1942**

Synonyms: *Squalonchocotyle sphyrnae* MacCallum, 1931.

Records: On the gills of the smooth hammerhead, Woods Hole, Massachusetts (MacCallum, 1931).

Remarks: Also reported from *S. zygaena* and *S. diplana* off Senegal (Euzet and Maillard, 1967) and from *S. lewini*, off Hawaii (Yamaguti, 1968). Redescribed by Price (1942).

***Hexabothrium musteli* (MacCallum, 1931) Price, 1942**

Synonyms: *Acanthonchocotyle musteli* MacCallum, 1931, and *Onchocotyle musteli* (MacCallum, 1931) Dollfus, 1937.

Records: On the gills of the smooth dogfish, *Mustelus canis*, Woods Hole, Massachusetts (MacCallum, 1931).

Remarks: Euzet and Maillard (1967) reported it from Senegal and Lion Gulf, Mediterranean Sea. Lopez-Roman and De Armas (1987) provided morphological and SEM micrographs of this species from hosts around the Canary Islands. It was redescribed by Price (1942) and Maillard (1972). Boeger and Kritsky (1989) considered this species incertae sedis.

***Rajonchocotyle laevis* Price, 1942**

Synonyms: None.

Records: On the gills of the barndoor skate, *Raja laevis*, Woods Hole (Price, 1942).

Remarks: This species was described from a single specimen.

***Squalonchocotyle abbreviata* (Olsson, 1876) Cerfontaine, 1899**

Synonyms: *Onchocotyle abbreviata* Olsson, 1876, and *Erpocotyle abbreviata* Price, 1942.

Records: On the gills of spiny dogfish, Atlantic coast of Canada (Threlfall, 1969).

Remarks: I include this species because the record is near the geographic range of the manual. It is also known from the Irish Sea; Norway; Peter the Great Bay, Russia; Roscoff, France; the Atlantic Ocean; and the North Sea.

***Squalonchocotyle squali* MacCallum, 1931**

Synonyms: *Squalonchocotyle acanthi* MacCallum, 1931, and *Erpocotyle squali* Price, 1942.

Records: On the gills of the spiny dogfish, Woods Hole, Massachusetts (MacCallum, 1931).

Remarks: Redescribed by Price (1942). Also reported from New Zealand and the Black Sea.

Superfamily MAZOCRAEOIDEA (Bychowsky, 1957) emend. Beverley-Burton, 1984

Family ANTHOCOTYLIDAE Bychowsky, 1957

***Anthocotyle merluccii* van Beneden and Hesse, 1863**

Synonyms: *Anthocotyle merluccii americanus* MacCallum, 1916b, and *A. americanus* (MacCallum, 1916b) Price, 1943b.

Records: On the gills of silver hake, *Merluccius bilinearis*, New Jersey (Meyers, 1978), Woods Hole, Massachusetts (MacCallum, 1916b); offshore hake, *M. albidus*, off Chesapeake Bay and New Jersey (new host record).

Remarks: Also reported from silver hake in Canada and from hakes (Gadidae) in the eastern, southeastern, and southwestern Atlantic Ocean; Mediterranean Sea; and the eastern Pacific Ocean off Eureka, California; the Strait of Georgia, Canada; and Peru. Redescribed by Price (1943b). Llewellyn (1956) described the microecology as well as adhesive attitude, and in 1963 he described larval development. Lyons (1966) studied histochemistry of the sclerites.

Family AXINIDAE Unnithan, 1957

***Axine hyporhampi* Price, 1962a**

Synonyms: *Axinoides hyporhampi* of Kingston et al. (1969) and of Zwerner and Lawler (1972).

Records: On the gills of the silverstripe halfbeak, *Hyporhamphus unifasciatus*, Chesapeake Bay (Kingston et al., 1969) and Woods Hole, Massachusetts (Price, 1962a).

Remarks: None.

***Nudaciraxine gracilis* (Linton, 1940) Price, 1962a**

Synonyms: *Axine gracilis* Linton, 1940, and *Axinoides gracilis* (Linton, 1940) Sproston, 1946.

Records: On the gills of Atlantic needlefish, Chesapeake Bay (McMahon, 1964; Kingston et al., 1969) and Woods Hole, Massachusetts (Linton, 1940).

Remarks: Hargis (1956c) reported this species at Alligator Harbor, Florida. Redescribed by Price (1962a). Kingston et al. (1969) described the oncomiracidium.

Family DICLIDOPHORIDAE Fuhrmann, 1928

***Absonifibula bychowskyi* Lawler and Overstreet, 1976**

Synonyms: None.

Records: On gills of the Atlantic croaker, Chesapeake Bay and Pamlico Sound, North Carolina (Thoney, 1991).

Remarks: Originally described from this host in Mississippi Sound.

***Choricotyle aspinachorda* Hargis, 1955h**

Possible synonym: *Diclidophora* sp. of Linton (1905).

Records: On the gills of the pigfish, *Orthopristis chrysoptera,* Chesapeake Bay (Kingston et al., 1969) and Beaufort, North Carolina (Linton, 1905).

Remarks: Hargis (1955h) described the species from Alligator Harbor, Florida, specimens. It has been reported from *O. ruber* in Venezuela (Bashirullah and Rado, 1987). According to Hargis (1959) this species may be a synonym of *C. caudalis* Koratha, 1955b.

***Choricotyle louisianensis* Hargis, 1955h**

Synonyms: None.

Records: On the gills of the northern kingfish, *Menticirrhus saxatilis,* off Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: The type host is the southern kingfish, *M. americanus,* from Louisiana. It was also reported from Puntarenas, Costa Rica.

***Diclidophora denticulata* (Olsson, 1876) Price, 1943a**

Synonyms: *Octobothrium denticulatum* Olsson, 1876; *Diclidophora carbonarii* Cerfontaine, 1895; and *Dactylocotyle denticulata* (Olsson, 1876) Cerfontaine, 1895.

Records: On the gills of the pollock, *Pollachius virens,* Woods Hole, Massachussets (Linton, 1900).

Remarks: Also reported from Canada, Ireland, Scotland, England (but see Llewellyn et al., 1980), the North Sea, France, the Barents Sea, and the Mediterranean Sea. Redescribed by Price (1943a). Its life cycle and biology were described by Frankland (1955). Sproston (1945b) and Llewellyn (1958) described the gill clamping mechanism. Egg hatching rhythm was studied by MacDonald (1975). Vitelline cell histochemistry was reported by Halton et al. (1974) and amino acid composition by Arme (1977). Llewellyn and Tully (1969) assessed speciation in diclidophorans and their gadid hosts.

***Diclidophoroides maccallumi* Price, 1943a**

Synonyms: *Dactylocotyle phycidis* of Stafford (1904); *Dactylocotyle minor* of Manter (1926); *Diclidophora maccallumi* (Price, 1943a) Sproston, 1946; and *Choricotyle merlangi* (MacCallum, 1917) Llewellyn, 1941.

Records: On the gills of red hake, *Urophycis chuss,* Mount Desert Island, Maine (Manter, 1925 and 1926), New Jersey (Meyers, 1978); spotted hake, *U. regia,* Chesapeake Bay (Kingston et al., 1969) and North Carolina (Suydam, 1971); on silver hake, Woods Hole, Massachusetts (MacCallum, 1917).

Remarks: Redescribed by Price (1943a) from *U. chuss* and by Rubec (1991) from Canadian *U. chesteri.* Suydam (1971) described the microecology of this species on host gills.

***Neoheterobothrium affine* (Linton, 1898) Price, 1943a**

Synonyms: *Octoplectanum affine* Linton, 1898; *Diclidophora affinis* (Linton, 1898) Linton, 1901; *Choricotyle affine* (Linton, 1898) Llewellyn, 1941, not *Heterobothrium affine* of Nagibina, 1953.

Records: On the gills and in mouth of summer flounder, *Paralichthys dentatus,* Chesapeake Bay (Jansen and Burreson, 1990), New Jersey (Meyers, 1978), and Woods Hole, Massachusetts (Linton, 1898).

Remarks: Also reported from the mouth of the southern flounder, *P. lethostigma,* Louisiana. Redescribed by Price (1943a). Mamaev (1987) redefined the genus.

***Neoheterobothrium cynoscioni* (MacCallum, 1917) Price, 1943a**

Synonyms: *Diclidophora cynoscioni* MacCallum, 1917; *Choricotyle cynoscioni* (MacCallum, 1917) Llewellyn, 1941; and *C. reynoldsi* Frayne, 1943.

Records: On the gills of weakfish, *Cynoscion regalis,* Chesapeake Bay (Frayne, 1943; Kingston et al., 1969), Woods Hole, Massachusetts (MacCallum, 1917); spotted seatrout, Chesapeake Bay (Frayne, 1943).

Remarks: Also reported from silver seatrout, *C. nothus,* in Florida and Louisiana; spotted seatrout and sand seatrout, *C. arenarius,* mouth, gills, and skin, Mississippi; and grunts (Haemulidae), Venezuela. Redescribed by Price (1943a) and Frayne (1943).

***Orbocotyle prionoti* (MacCallum, 1917) Euzet and Suriano, 1975**

Synonyms: *Diclidophora prionoti* MacCallum, 1917; *Cyclocotyla prionoti* (MacCallum, 1917) Price, 1943a; and *Choricotyle prionoti* (MacCallum, 1917) Llewellyn, 1941.

Records: On the gills of the northern searobin, *Prionotus carolinus,* Woods Hole, Massachusetts (MacCallum, 1917); striped searobin, *P. evolans,* off Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Hargis (1955h) reported this species from the leopard searobin, *P. scitulus,* in Florida and Louisiana. Redescribed by Price (1943a).

***Pedocotyle minima* Hargis, 1955h**

Synonyms: None.

Records: On the gills of silver perch, Chesapeake Bay (Kingston et al., 1969).

Remarks: The species was described from Alligator Harbor, Florida, hosts. Kingston et al. (1969) described the oncomiracidium.

***Pedocotyle morone* (MacCallum, 1913c) MacCallum, 1913d**

Synonyms: *Podocotyle morone* MacCallum, 1913c.

Records: On the gills of white perch, New York City fish market (MacCallum, 1913c).

Remarks: Hargis (1955h) questioned the validity of this host record. The species was redescribed by Price (1943a).

Family DISCOCOTYLIDAE Price, 1936

***Bicotylophora trachinoti* (MacCallum, 1921) Price, 1936**

Synonyms: *Dactylocotyle trachinoti* MacCallum, 1921.

Records: On the gills of Florida pompano, *Trachinotus carolinus*, Chesapeake Bay (McMahon, 1963).

Remarks: Also reported from Alligator Harbor, Florida, as well as Mississippi, Mexico, Venezuela, and Uruguay; on permit, *T. falcatus*, Mexico and the Ivory Coast; and on the gafftopsail pompano, *T. rhodopus*, Mexico. Redescribed by McMahon (1963), Caballero and Bravo-Hollis (1965), as well as Nasir and Fuentes Zambrano (1983). Lawler (1977) mentioned its role as a pest in aquaculture. Kohn et al. (1992) provided measurements and SEM micrographs of this species from Brazilian *T. carolinus*.

Family GASTROCOTYLIDAE Price, 1943a

***Gotocotyla acanthophallus* (MacCallum and MacCallum, 1913) Yamaguti, 1963**

Synonyms: *Microcotyle acanthophallus* MacCallum and MacCallum, 1913, and *Lithidocotyle acanthophallus* (MacCallum and MacCallum, 1913) Sproston, 1946, and of Hargis (1956d).

Records: On the gills of bluefish, *Pomatomus saltatrix*, Chesapeake Bay (McMahon, 1964; Kingston et al., 1969); king mackerel, *Scomberomorus cavalla*, Chesapeake Bay (Zwerner and Lawler, 1972); Spanish mackerel, *S. maculatus*, Chesapeake Bay (McMahon, 1964); and striped bass, *Morone saxatilis*, Atlantic Ocean (New York City fish market) (MacCallum and MacCallum, 1913).

Remarks: Also reported from mackerels (Scombridae) in Florida, Louisiana, and Mexico. Hargis (1956c) considered the striped bass to be an accidental host.

***Pseudaxine mexicana* Meserve, 1938**

Probable synonym: *Pseudaxine texana* Koratha, 1955b.

Records: On the gills of Spanish mackerel, Chesapeake Bay (McMahon, 1964).

Remarks: Also reported from mackerels in Florida, Louisiana, Texas, and Mexico. Redescribed by Bravo-Hollis (1953). Dillon and Hargis (1965b) emended the generic diagnosis. Lebedev (1986) removed this species to the monotypic genus *Mexicotyle*. Bravo-Hollis (1989) gave new Mexican collecting localities and compared the gastrocotylid species of the Atlantic and Pacific Oceans off Mexico.

Family HETERAXINIDAE Price, 1962b

Mamaev (1990) provided a systematic list of members of this and related families under the suborder Microcotylinae.

***Cemocotyle carangis* (MacCallum, 1913c) Sproston, 1946**

Synonyms: *Microcotyle carangis* MacCallum, 1913c, and *Gotocotyla carangis* (MacCallum, 1913c) Meserve, 1938.

Records: On the gills of blue runner, *Caranx crysos*, Woods Hole, Massachusetts (MacCallum, 1913c)

Remarks: Also reported at Alligator Harbor, Florida, and Veracruz, Mexico. Redescribed by Price (1962b). Bravo-Hollis and Salgado-Maldonado (1983) provided new morphological data on specimens collected from Mexican *C. crysos*.

***Cemocotyle noveborancensis* (MacCallum, 1918) Sproston, 1946**

Synonyms: *Axine carangis* MacCallum, 1918, *A. (Heteraxine) carangis* (MacCallum, 1918) Yamaguti, 1938, and *Heteraxine carangis* (MacCallum, 1918) Yamaguti, 1938.

Records: On the gills of crevalle jack, *Caranx hippos*, New York region (MacCallum, 1918).

Remarks: Also reported from Alligator Harbor, Florida, and Campeche, Mexico. Redescribed by Price (1962b). Bravo-Hollis and Salgado-Maldonado (1983) gave new morphological data on specimens from Mexican *C. hippos*.

***Heteraxinoides xanthophilis* (Hargis, 1956c) Yamaguti, 1963**

Synonyms: *Heteraxine xanthophilis* Hargis, 1956c, and *Heteraxinoides xanthophiloides* Price, 1962b.

Records: On the gills of spot, *Leiostomus xanthurus*, Chesapeake Bay (Kingston et al., 1969; Thoney, 1988, a and b, 1991), Pamlico Sound, North Carolina (Thoney, 1991), and Woods Hole, Massachusetts (Price, 1962b).

Remarks: Also reported from Florida (Hargis, 1956c) and Texas (Joy, 1976). Kingston et al. (1969) described the oncomiracidium. Thoney (1988a) showed its developmental variation on hosts of different sizes and (1988b) studied egg and oncomiracidial structures. Thoney (1991) discussed population dynamics of this and other parasites on juvenile spot.

Family HEXOSTOMATIDAE Price, 1936

***Hexostoma lintoni* Price, 1961a**

Synonyms: *Hexacotyle thynni* of Linton (1901).

Records: In the mouth of Atlantic bonito, *Sarda sarda*, Woods Hole, Massachusetts (Linton, 1901 and 1940).

Remarks: Price (1961a) redescribed this species from a single specimen.

***Neohexostoma euthynni* (Meserve, 1938) Price, 1961a**

Synonyms: *Hexostoma euthynni* Meserve, 1938, and *H. macracanthum* Fujii, 1944.

Records: On the gills of little tunny, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported from scombrids at the Tortugas, Florida; Baja California; Galapagos Islands; Great Barrier Reef, Australia; and the South China Sea. Redescribed by Millemann (1956). Rohde (1978a) considered this genus to be synonymous with *Hexostoma*. Rohde (1980) described some aspects of its cecal ultrastructure.

Family MACROVALVITREMATIDAE Yamaguti, 1963

***Hargisia bairdiella* (Hargis, 1956a) Yamaguti, 1963**

Synonyms: *Tagia bairdiella* Hargis, 1956a.

Records: On the gills of silver perch, Chesapeake Bay (McMahon, 1963; Kingston et al., 1969).

Remarks: First described from Alligator Harbor, Florida, by Hargis (1956a).

***Macrovalvitrematoides micropogoni* (Pearse, 1949) Yamaguti, 1963**

Synonyms: *Tagia micropogoni* Pearse, 1949.

Records: On the gills of Atlantic croaker, Chesapeake Bay (Kingston et al., 1969) and Beaufort, North Carolina (Pearse, 1949).

Remarks: Also reported from Florida, Mississippi, and Texas (Joy and Price, 1976). Redescribed by Hargis (1956a). Kingston et al. (1969) described the oncomiracidium. Bravo-Hollis (1981) erected the subfamily Macrovalvitrematinae containing this genus.

***Pseudotagia cupida* (Hargis, 1956a) Yamaguti, 1963**

Synonyms: *Tagia cupida* Hargis, 1956a.

Records: On the gills of pigfish, Chesapeake Bay (Kingston et al., 1969), off North Carolina (Suydam, 1971).

Remarks: Hargis (1956a) described the species from Alligator Harbor, Florida. The species was redescribed by Kohn et al. (1984) from bluestriped grunts, *Haemulon sciurus*, and Kohn et al. (1992) gave a new host record for Brazil.

Family MAZOCRAEIDAE Price, 1936

Mamaev (1982a) reviewed the systematics of several genera within the family.

***Clupeocotyle brevoortia* Hargis, 1955f**

Synonyms: *Dactylocotyle* sp. of Linton (1905); *Diclidophora lintoni* Koratha, 1955b; *Clupeocotyle lintoni* (Koratha, 1955b) Hargis, 1959; and probably *Diclodophora* sp. [sic] of Westman and Nigrelli, 1955.

Records: On the gills of Atlantic menhaden, *Brevoortia tyrannus*, Beaufort, North Carolina (Linton, 1905), Chesapeake Bay (McMahon, 1963), New Jersey, and Long Island (Westman and Nigrelli, 1955).

Remarks: Also reported from gulf menhaden, *B. patronus*, in Florida and Texas. Redescribed by McMahon (1963).

***Grubea cochlear* Diesing, 1858**

Synonyms: *Pleurocotyle scombri* Linton, 1940, and *Grubea pneumatophori* Price, 1961b.

Records: On the gills of the chub mackerel, *Scomber japonicus*, Woods Hole, Massachusetts (Linton, 1940).

Remarks: Also reported from mackerels from Brazil, the Mediterranean Sea, the Portuguese coast, and the Patagonian shelf of the southwest Atlantic Ocean. Wagner (1975) provided some comparative measurements for species in this genus. Mamaev (1982b) redefined the genus and redescribed the species. Rohde (1987a) summarized global locality data and redescribed the species.

***Kuhnia scombri* (Kuhn, 1829) Sproston, 1945a**

Synonyms: *Octostoma scombri* Kuhn, 1829.

Records: On the gills of Atlantic mackerel, *Scomber scombrus*, Chesapeake Bay (Price, 1961b); Newport, Rhode Island (Goto, 1899); off Cape Hatteras, North Carolina (Romuk-Wodoracki, 1988); and Woods Hole, Massachusetts (Price, 1961b).

Remarks: Also reported on mackerels from Canada, the eastern and southwestern Atlantic Ocean, Mediterranean Sea, eastern and southwestern Pacific Ocean, and Hawaii. This is a cosmopolitan species on mackerels. Rohde (1989) summarized the known geographical distribution of *Kuhnia* spp. from *Scomber* spp. The species was redescribed by Price (1961b) and by Nasir and

Fuentes Zambrano (1983). Sproston (1945a) and Llewellyn (1957) described the anatomy of the clamping mechanism on host gills; Llewellyn (1956), the gill microecology and (1963) larval development; and Euzet (1957), the oncomiracidium. Finlayson (1982) provided detailed information on the reproductive processes of this species. Rohde (1991) and Rohde and Watson (1985) studied geographic variation in morphology and microhabitat in *Kuhnia*. Rohde (1987b) studied sclerite morphology. Mamaev and Parukhin (1986) revised the genus composition and provided a table of comparative characteristics of *Kuhnia* spp.

***Mazocraeoides georgei* Price, 1936**

Synonyms: None.

Records: On the gills of blueback herring, *Alosa aestivalis*, Chesapeake Bay (Zwerner and Lawler, 1972); hickory shad, *A. mediocris*, Woods Hole, Massachusetts (Linton, 1940); alewife, *A. pseudoharengus*, Chesapeake Bay (Zwerner and Lawler, 1972), New Jersey (Meyers, 1978), and Woods Hole, Massachusetts (Linton, 1940); and Atlantic menhaden, Chesapeake Bay (McMahon, 1963).

Remarks: Hargis (1955g) and McMahon (1963) redescribed the species (but see below). Zwerner and Lawler (1972) suggested that the oncomiracidium described by Kingston et al. (1969) was probably that of this species. Kohn and Portes Santos (1988) provided measurements and illustrations from Brazilian clupeid fishes.

***Mazocraeoides hargisi* Price, 1961b**

Possible synonyms: *Mazocraeoides georgei* of Hargis (1955g) and McMahon (1963).

Records: On the gills of Atlantic menhaden, Chesapeake Bay (Kingston et al., 1969).

Remarks: Kingston et al. (1969) described the oncomiracidium. Zwerner and Lawler (1972) questioned this record and suggested that it was *M. georgei*. Kohn and Portes Santos (1988) considered this to be a synonym of *M. georgei*.

***Mazocraeoides olentangiensis* Sroufe, 1958**

Synonyms: *Mazocraeoides similis* Price, 1958.

Records: On the gills of gizzard shad, *Dorosoma cepedianum*, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Originally described from shad in the Olentangy River, Ohio (Sroufe, 1958). It is also known from Lake Erie; Norris and Reelfoot Lakes, Tennessee; and the Tennessee River, Alabama. Wright and Dechtier (1974) described light and SEM features of surface structures. Kohn and Portes Santos (1988) synonymized this with *M. georgei*. This is primarily a freshwater species that is also found in slightly brackish estuarine waters.

Family MICROCOTYLIDAE Taschenberg, 1879

Mamaev (1986) presented a brief summary of the taxonomic system for the family.

***Cynoscionicola heteracantha* (Manter, 1938) Price, 1962b**

Synonyms: *Microcotyle heteracantha* Manter, 1938, and *Microcotyle* sp. of Linton (1905 and 1940).

Records: On the gills of spotted seatrout, Chesapeake Bay (Zwerner and Lawler, 1972), and Beaufort, North Carolina (Manter, 1938); weakfish, Woods Hole, Massachusetts (Linton, 1940), Chesapeake Bay (Kingston et al., 1969), and Beaufort, North Carolina (Linton, 1905).

Remarks: Also reported from spotted seatrout collected at Alligator Harbor, Florida (Hargis, 1956b). Kingston et al. (1969) described the oncomiracidium. Lambert and Euzet (1979) reviewed the genus.

***Cynoscionicola pseudoheteracantha* (Hargis, 1956b) Price, 1962b**

Synonyms: *Microcotyle pseudoheteracantha* Hargis, 1956b.

Records: On the gills of silver seatrout, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Originally described from Louisiana hosts.

***Gamacallum macroura* (MacCallum and MacCallum, 1913) Unnithan, 1971**

Synonyms: *Microcotyle macroura* MacCallum and MacCallum, 1913.

Records: On the gills of striped bass, Chesapeake Bay (Zwerner and Lawler, 1972), Atlantic coast of the U.S. (MacCallum and MacCallum, 1913).

Remarks: None.

***Metamicrocotyla macracantha* (Alexander, 1954) Koratha, 1955b**

Synonyms: *Microcotyle macracantha* Alexander, 1954.

Records: On the gills of striped mullet, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported from Georgia (Rawson, 1976); Biscayne Bay, Florida (Skinner, 1975); U.S. Gulf of Mexico coast; Puerto Rico; and the Pacific Ocean in the Gulf of California, Mexico, and Peru. Redescribed by Hargis (1956b) and also by Kohn et al. (1994), who redescribed the species from Brazilian *Mugil liza*. Garcia and Williams (1985) gave some temporal data on this species from Puerto Rico.

***Microcotyle archosargi* MacCallum, 1931**

Synonyms: None.

Records: On the gills of sheepshead from the New York City fish market (MacCallum, 1931).

Remarks: Also reported from Alligator Harbor, Florida (Hargis, 1956b).

***Microcotyle centropristis* MacCallum, 1915**

Synonyms: None.

Records: On the gills of black sea bass, *Centropristis striata*, New York City fish market (MacCallum, 1915).

Remarks: None.

***Microcotyle eueides* MacCallum and MacCallum, 1913**

Synonyms: None.

Records: On the gills of striped bass along the northwestern Atlantic coast (MacCallum and MacCallum, 1913).

Remarks: None.

***Microcotyle hiatulae* Goto, 1894**

Synonyms: *Microcotyle furcata* Linton, 1940.

Records: On the gills of tautog, *Tautoga onitis*, Newport, Rhode Island (Goto, 1899), Woods Hole (Linton, 1940), and the mouth of Chesapeake Bay (Thoney and Munroe, 1987).

Remarks: Thoney and Munroe (1987) redescribed the species and gave comments on its postlarval development.

***Microcotyle longicauda* Goto, 1899**

Synonyms: *Cynoscionicola longicauda* (Goto, 1899) Yamaguti, 1963.

Records: On the gills of weakfish, Newport, Rhode Island (Goto, 1899).

Remarks: None.

***Microcotyle otrynteri* Pearse, 1949**

Synonyms: None.

Records: On the gills of longspine porgy, *Stenotomus caprinus*, Beaufort, North Carolina (Pearse, 1949).

Remarks: The species is poorly described and needs further investigation.

***Microcotyle peprili* Pearse, 1949**

Synonyms: None.

Records: On the gills of harvestfish, *Peprilus alepidotus*, Chesapeake Bay (McMahon, 1964; Kingston et al., 1969), and Beaufort, North Carolina (Pearse, 1949).

Remarks: Redescribed by McMahon (1964).

***Microcotyle pomatomi* Goto, 1899**

Synonyms: *Microcotyle australiensis* MacCallum, 1921; *M. debueni* Mañe-Garzon, 1959; and *M. temnodontis* Sandars, 1945.

Records: On the gills of bluefish, Beaufort (Linton, 1905; Pearse, 1949) and Hatteras, North Carolina (Anderson, 1970); Chesapeake Bay (McMahon, 1964); New Jersey (Meyers, 1978); Newport, Rhode Island (Goto, 1899); and Woods Hole, Massachusetts (Linton, 1901 and 1940).

Remarks: Although widely distributed along the Atlantic and Gulf coasts of the United States, *M. pomatomi* has also been reported from the Portuguese coast; Walvis Bay, Namibia; the Black Sea; and Australia. It was redescribed by Koratha (1955b), McMahon (1964), and Williams (1991) who also gave comparative measurements from various authors and discussed the taxonomy of this species. Anderson (1970) reported the geographic range of this species along the U.S. Atlantic coast.

***Microcotyle poronoti* MacCallum, 1915**

Synonyms: None.

Records: On the gills of butterfish, *Peprilus triacanthus*, Chesapeake Bay (McMahon, 1964; Kingston et al., 1969), New Jersey (Meyers, 1978), and Woods Hole, Massachusetts (MacCallum, 1915, Linton, 1940).

Remarks: Also reported from butterfish in Canada. Redescribed by McMahon (1964). Kingston et al. (1969) described the oncomiracidium.

***Microcotyle stenotomi* Goto, 1899**

Synonyms: None.

Records: On the gills of scup, *Stenotomus chrysops*, Woods Hole, Massachusetts (Linton, 1940); Newport, Rhode Island (Goto, 1899); Chesapeake Bay (McMahon, 1964); and off North Carolina (Suydam, 1971).

Remarks: MacCallum (1913a) briefly described fertilization and egg laying. Suydam (1971) described the distribution of worms on gill arches.

***Pauciconfibula pogoniae* (MacCallum, 1913c) Chisholm, Beverley-Burton, and McAlpine, 1991**

Synonyms: *Microcotyle pogoniae* MacCallum, 1913c; *Aspinatrium pogoniae* (MacCallum, 1913c) Yamaguti, 1963; and *Pseudoaspinatrium pogoniae* (MacCallum, 1913c) Mamaev, 1986.

Records: On the gills of black drum, *Pogonias cromis*, New York region (MacCallum, 1913c).

Remarks: Also reported from Alligator Harbor, Florida, by Hargis (1956b). Chisholm et al. (1991) emended the generic diagnosis.

Family NEOTHORACOCOTYLIDAE Lebedev, 1969

***Neothoracocotyle acanthocybii* (Meserve, 1938) Hargis, 1956d**

Synonyms: *Gotocotyla acanthocybii* Meserve, 1938.

Records: On the gills of wahoo, *Acanthocybium solandri*, offshore from Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: *Neothoracocotyle acanthocybii* was described from the Galapagos Islands and has been reported from Hawaii; off Noumea, New Caledonia; and from

the Great Barrier Reef. Yamaguti (1968) redescribed the species.

***Scomberocotyle scomberomori* (Koratha, 1955b) Hargis, 1956d**

Synonyms: *Microcotyle scomberomori* Koratha, 1955b.

Reports: On the gills of king mackerel (Zwerner and Lawler, 1972) and Spanish mackerel, Chesapeake Bay (McMahon, 1964).

Remarks: Also reported from the Gulf of Mexico off Florida and Texas.

***Thoracocotyle crocea* MacCallum, 1913b**

Synonyms: *Thoracocotyle paradoxica* Meserve, 1938, and possibly of Pearse, 1949.

Records: On the gills of Spanish mackerel, New York fish market (MacCallum, 1913b), Chesapeake Bay (McMahon, 1964; Kingston et al., 1969); and king mackerel, Beaufort, North Carolina (Pearse, 1949).

Remarks: Also reported from Florida and Mexico. Redescribed by McMahon (1964).

Family PROTOMICROCOTYLIDAE Poche, 1926

***Protomicrocotyle mirabilis* (MacCallum, 1918) Johnston and Tiegs, 1922**

Synonyms: *Acanthodiscus mirabilis* MacCallum, 1918.

Records: On the gills of crevalle jack, Chesapeake Bay (Zwerner and Lawler, 1972).

Remarks: Also reported on crevalle jack from Alligator Harbor, Florida; Texas; and the Ivory Coast; and from the horse-eye jack, *Caranx latus*, Mexico. Redescribed by Koratha (1955b) and by Caballero and Bravo-Hollis (1965). Bashirullah and Rodriguez (1992) analyzed the distribution of *P. mirabilis* and other monogenean species on the gill arches of Venezuelan *C. hippos*.

Family PYRAGRAPHORIDAE Yamaguti, 1963

***Pyragraphorus pyragraphorus* (MacCallum and MacCallum, 1913) Sproston, 1946**

Synonyms: *Microcotyle pyragraphorus* MacCallum and MacCallum, 1913.

Records: On the gills of Florida pompano, Atlantic coast of the United States (MacCallum and MacCallum, 1913).

Remarks: Also reported from Baja California, Mexico (Bravo-Hollis, 1978), and the Great Barrier Reef, Australia. Redescribed by Hargis (1956b). Bravo-Hollis (1984) gave some comparative measurements.

Host-Monogenea List

This host-Monogenea list includes only those species on fishes occurring along the western Atlantic coast from the U.S.-Canada border to Beaufort, North Carolina. Hosts from more distant localities are not listed. Older host names mentioned in older Monogenea reports have been updated and are those given in the American Fisheries Society Special Publication No. 20 (Robins et al.,1991). Fish families and parasites are listed alphabetically within each order of fishes.

Class ELASMOBRANCHIOMORPHI
Order LAMNIFORMES

Family Alopiidae – thresher sharks
***Alopias vulpinus* – thresher shark**
Cathariotrema selachii

Family Carcharhinidae – requiem sharks
***Carcharhinus limbatus* – blacktip shark**
Dermophthirius penneri
Erpocotyle maccallumi

***Carcharhinus obscurus* – dusky shark**
Cathariotrema selachii
Dermophthirius carcharhini
Loimos salpinggoides
Microbothrium apiculatum

***Carcharhinus plumbeus* – sandbar shark**
Erpocotyle macrohystera

***Mustelus canis* – smooth dogfish**
Hexabothrium musteli

***Negaprion brevirostris* – lemon shark**
Neodermophthirius harkemai

***Rhizoprionodon terraenovae* – Atlantic sharpnose shark**
Loimos scoliodoni

Family Sphyrnidae – hammerhead sharks
***Sphyrna zygaena* – smooth hammerhead shark**
Cathariotrema selachii
Erpocotyle microstoma
Erpocotyle sphyrnae
Tristoma coccineum

Order SQUALIFORMES

Family Squalidae – dogfish sharks
***Squalus acanthias* – spiny dogfish**
Amphibdelloides maccallumi
Heterocotyle minima
Microbothrium apiculatum
Squalonchocotyle abbreviata
Squalonchocotyle squali

Order RAJIFORMES

Family *Dasyatidae* – stingrays
***Dasyatis americana* – southern stingray**
Monocotyle diademalis
Monocotyle pricei

***Dasyatis centroura* – roughtail stingray**
Dasybatotrema dasybatis
Entobdella bumpusii
Heterocotyle minima
Thaumatocotyle dasybatis

***Dasyatis say* – bluntnose stingray**
Loimopapillosum dasyatis
Monocotyle diademalis
Monocotyle pricei

Family Myliobatidae – eagle rays
***Aetobatis narinari* – spotted eagle ray**
Papillicotyle floridana

***Rhinoptera bonasus* – cownose ray**
Benedeniella posterocolpa

Family Rajidae – skates
***Raja eglanteria* – clearnose skate**
Empruthotrema raiae

***Raja erinacea* – little skate**
Empruthotrema raiae
Pseudacanthocotyla verrilli
Thaumatocotyle dasybatis

***Raja laevis* – barndoor skate**
Rajonchocotyle laevis

***Raja ocellata* – winter skate**
Empruthotrema raiae

***Raja radiata* – thorny skate**
Pseudacanthocotyla verrilli

Family Torpedinidae – electric rays
***Torpedo nobiliana* – Atlantic torpedo**
Amphibdella flavolineata
Amphibdelloides maccallumi

Class OSTEICHTHYES
Order ACIPENSERIFORMES

Family Acipenseridae – sturgeons
***Acipenser brevirostrum* – shortnose sturgeon**
Diclybothrium armatum
Nitzschia superba

***Acipenser oxyrhynchus* – Atlantic sturgeon**
Nitzschia sturionis
Nitzschia superba

Order CLUPEIFORMES

Family Clupeidae – herrings
***Alosa aestivalis* – blueback herring**
Mazocraeoides georgei

***Alosa mediocris* – hickory shad**
Mazocraeoides georgei

***Alosa pseudoharengus* – alewife**
Mazocraeoides georgei

***Brevoortia tyrannus* – Atlantic menhaden**
Clupeocotyle brevoortia
Mazocraeoides georgei
Mazocraeoides hargisi

***Dorosoma cepedianum* – gizzard shad**
Mazocraeoides olentangiensis

Order GADIFORMES

Family Gadidae – cods
***Gadus morhua* – Atlantic cod**
Udonella caligorum

***Merluccius albidus* – offshore hake**
Anthocotyle merluccii

***Merluccius bilinearis* – silver hake**
Anthocotyle merluccii
Diclidophoroides maccallumi

***Pollachius virens* – pollock**
Diclidophora denticulata

***Urophycis chuss* – red hake**
Diclidophoroides maccallumi

***Urophycis regia* – spotted hake**
Diclidophoroides maccallumi

Order ATHERINIFORMES

Family Belonidae – needlefishes
***Strongylura marina* – Atlantic needlefish**
Ancyrocephalus parvus
Nudaciraxine gracilis

Family Cyprinodontidae – killifishes
***Cyprinodon variegatus* – sheepshead minnow**
Fundulotrema prolongis
Gyrodactylus stephanus

***Fundulus heteroclitus* – mummichog**
Fundulotrema prolongis
Gyrodactylus stephanus
Swingleus sp.

***Fundulus majalis* – striped killifish**
Fundulotrema prolongis
Gyrodactylus stephanus
Swingleus sp.

Family Exocoetidae – flyingfishes
***Hyporhamphus unifasciatus* – silverstripe halfbeak**
Axine hyporhampi

Order SCORPAENIFORMES

Family Cyclopteridae – snailfishes
***Cyclopterus lumpus* – lumpfish**
Udonella caligorum

Family Triglidae – searobins
***Prionotus carolinus* – northern searobin**
Orbocotyle prionoti

***Prionotus evolans* – striped searobin**
Orbocotyle prionoti

Order PERCIFORMES

Family Carangidae – jacks
***Caranx crysos* – blue runner**
Cemocotyle carangis

***Caranx hippos* – crevalle jack**
Cemocotyle noveborancensis
Protomicrocotyle mirabilis

***Trachinotus carolinus* – Florida pompano**
Bicotylophora trachinoti
Pyragraphorus pyragraphorus

Family Echeneidae – remoras
***Echeneis naucrates* – sharksucker**
Dionchus agassizi
Dionchus remorae

***Remora brachyptera* – spearfish remora**
Dionchus agassizi

***Remora remora* – remora**
Dionchus agassizi

Family Ephippidae – spadefishes
***Chaetodipterus faber* – Atlantic spadefish**
Pseudohaliotrema longiphallus

Family Haemulidae – grunts
***Orthopristis chrysoptera* – pigfish**
Choricotyle aspinachorda
Pseudotagia cupida

Family Istiophoridae – billfishes
***Tetrapturus albidus* – white marlin**
Capsaloides cornutus
Capsaloides magnaspinosus
Tristomella laevis

Family Labridae – wrasses
***Tautoga onitis* – tautog**
Microcotyle hiatulae

Family Mugilidae – mullets
***Mugil cephalus* – striped mullet**
Haliotrema vanbenedeni
Metamicrocotyla macracantha

Family Percichthyidae – temperate basses
***Morone americana* – white perch**
Erpocotyle mavori ?
Onchocleidus nactus
Pedocotyle morone

***Morone saxatilis* – striped bass**
Gamacallum macroura
Gotocotyla acanthophallus
Microcotyle eueides

Family Pomatomidae – bluefishes
***Pomatomus saltatrix* – bluefish**
Gotocotyla acanthophallus
Microcotyle pomatomi

Family Sciaenidae – drums
***Bairdiella chrysoura* – silver perch**
Hargisia bairdiella
Pedocotyle minima
Rhamnocercus bairdiella

Cynoscion nebulosus – **spotted seatrout**
Cynoscionicola heteracantha
Diplectanum bilobatum
Neoheterobothrium cynoscioni

Cynoscion nothus – **silver seatrout**
Cynoscionicola pseudoheteracantha

Cynoscion regalis – **weakfish**
Cynoscionicola heteracantha
Microcotyle longicauda
Neoheterobothrium cynoscioni

Leiostomus xanthurus – **spot**
Heteraxinoides xanthophilis

Menticirrhus americanus – **southern kingfish**
Rhamnocercus stichospinus

Menticirrhus saxatilis – **northern kingfish**
Choricotyle louisianensis

Micropogonias undulatus – **Atlantic croaker**
Absonifibula bychowskyi
Macrovalvitrematoides micropogoni

Pogonias cromis – **black drum**
Pauciconfibula pogoniae

Family Scombridae – mackerels
Acanthocybium solandri – **wahoo**
Neothoracocotyle acanthocybii

Euthynnus alletteratus – **little tunny**
Caballerocotyla manteri
Neohexostoma euthynni
Tristomella onchidiocotyle
Udonella caligorum

Katsuwonus pelamis – **skipjack tuna**
Tristomella lintoni

Sarda sarda – **Atlantic bonito**
Hexostoma lintoni

Scomber japonicus – **chub mackerel**
Grubea cochlear

Scomber scombrus – **Atlantic mackerel**
Kuhnia scombri

Scomberomorus cavalla – **king mackerel**
Gotocotyla acanthophallus
Scomberocotyle scomberomori
Thoracocotyle crocea

Scomberomorus maculatus – **Spanish mackerel**
Gotocotyla acanthophallus
Pseudaxine mexicana
Scomberocotyle scomberomori
Thoracocotyle crocea

Thunnus albacares – **yellowfin tuna**
Nasicola klawei

Family Serranidae – sea basses
Centropristis striata – **black sea bass**
Microcotyle centropristis

Family Sparidae – porgies
Archosargus probatocephalus – **sheepshead**
Microcotyle archosargi
Monocotyle pricei?

Stenotomus caprinus – **longspine porgy**
Microcotyle otrynteri

Stenotomus chrysops – **scup**
Microcotyle stenotomi

Family Stromateidae – butterfishes
Peprilus alepidotus – **harvestfish**
Microcotyle peprili

Peprilus triacanthus – **butterfish**
Microcotyle poronoti

Family Xiphiidae – swordfishes
Xiphias gladius – **swordfish**
Tristoma coccineum
Tristoma integrum
Tristomella laevis

Order PLEURONECTIFORMES

Family Bothidae – lefteye flounders
Paralichthys dentatus – **summer flounder**
Neoheterobothrium affine

Scophthalmus aquosus – **windowpane**
Bothitrema bothi

Family Pleuronectidae – righteye flounders
Hippoglossus hippoglossus – **Atlantic halibut**
Entobdella hippoglossi

Pleuronectes putnami – **smooth flounder**
Protancyrocephaloides liopsettae

Order TETRAODONTIFORMES

Family Molidae – molas
***Mola mola* – ocean sunfish**
Capsala martinierei
Tricotyla molae

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Sherman S. Hendrix's interest in the marine environment began as he grew up near Long Island Sound in Connecticut. After completing his undergraduate education at Gettysburg College, he pursued interests in parasitology in the course of obtaining a M.S. degree at Florida State University. While at FSU, he was a member of the scientific crew aboard the USNS *Eltanin* on one of its cruises to the Antarctic Ocean. After obtaining a Ph.D. at the University of Maryland, College Park, he returned to the study of the systematics and ecology of marine fish parasites, particularly aspidogastrid trematodes and Monogenea, while teaching biology at Gettysburg College.

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